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SELECTION AND POPULATION STRUCTURE IN *LOLIUM*

IV. CORRELATED RESPONSE TO SELECTION

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1. INTRODUCTION

EARLIER papers in this series have analysed the genetic control and response to selection of a single character, date of ear emergence, in two outbreeding populations of *L. perenne* (Cooper, 1959*a* and *b*). It was concluded that most of the variation in this character was genetic and additive, that all parents were highly heterozygous, and that considerable response to selection was possible.

In the same material, records were also taken on a number of ear characters to see whether they revealed a similar genetic structure, and to detect any correlated response to selection for ear emergence. The heritability of each character has been estimated from the analysis of clonal replicates and from parent/progeny regression, and its correlated responses to selection under the different mating systems has been assessed.

2. MATERIAL AND METHODS

Operational details of the selection experiment in 1956 and 1957 have been given earlier (Cooper, 1959*b*). In each year, the original populations and selection lines were grown as seedlings, and the selected parents in each generation were put out as clonal replicates.

In 1956, records of ear characters were taken on one replicate only of the clonal material, which consisted of original population plants of Irish and Kent ryegrass, and the parents of the first two generations of selection. In 1957, records were taken on all replicates of the clonal material, on three different samples of Irish and Kent ryegrasses, and on the seedling progenies of the three generations of selection. Eighty seedlings were measured from each population and ten from each progeny.

The methods of harvesting and recording were the same for both years. Three heads were harvested, soon after anthesis, from the first flush of heading on each plant. By the time anthesis begins, all the characters measured have reached their maximum dimensions, and further delay in harvesting may result in seed shedding. The heads were air-dried in a greenhouse, and the following measurements taken on each, as illustrated in fig. 1.

(1) *total length*, from the flag-leaf node to the tip of the inflorescence,
(2) *ear length*, from the insertion of the lowest spikelet to the tip of the inflorescence,
(3) *number of spikelets*,

and, measured on the sixth spikelet from the tip,

(4) *length of empty glume*,
(5) *length of spikelet*,
(6) *number of florets per spikelet*.

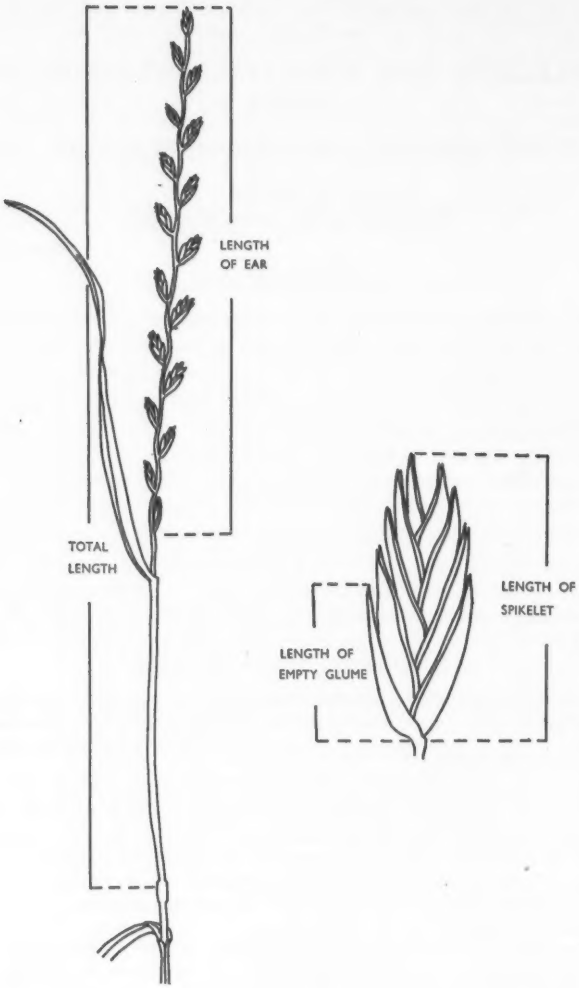

FIG. 1.—Ear characters recorded in the present work.

3. POPULATION DIFFERENCES

A comparison of ear characters in samples of Irish and Kent ryegrasses in 1957 is given in table 1, which includes date of ear emergence for comparison. In no cases were block differences or sample/block interactions significant.

In spite of about four weeks' difference between Irish and Kent in ear emergence, no significant differences were recorded for total length, length of empty glume or length of spikelet. Kent possessed longer ears and more spikelets than Irish, but fewer florets per spikelet. Even so the total number of florets per inflorescence was greater in Kent ryegrass. No differences between samples were noted in Kent, but in Irish one sample (Ba 6650) had slightly longer ears, more spikelets and fewer florets than the others.

A further comparison is possible using clonal replicates of Irish and Kent ryegrasses in 1956 and 1957; this also provides an estimate of the repeatability of the measurements from year to year (table 2).

TABLE 1

Ear characters in Irish and Kent ryegrass populations 1957

	Irish				Kent				5 per cent. sig. diff. for	
	Ba 6650	Ba 6773	Ba 6738	Mean	Ba 6622	Ba 6740	Ba 6565	Mean	Samples	Means
Total length (cm.)	52·8	51·2	50·6	51·5	51·9	51·7	52·4	52·0	N.S.	N.S.
Length of ear (cm.)	24·1	22·9	23·0	23·3	24·4	24·9	25·1	24·8	1·06	0·61
No. of spikelets	24·8	23·8	22·9	23·8	28·1	27·4	27·7	27·7	1·24	0·72
Length of spikelet (mm.)	15·0	15·2	15·9	15·4	15·1	15·6	15·3	15·3	N.S.	N.S.
Length of empty glume (mm.)	10·3	10·2	10·0	10·2	10·7	10·2	10·5	10·4	N.S.	N.S.
No. of florets	10·1	10·8	10·9	10·6	9·9	10·1	9·9	10·0	0·45	0·26
Date of ear emergence	30·6 April	27·8 April	28·6 April	29·0 April	22·5 May	22·7 May	20·5 May	21·9 May	1·86	1·09

The clonal material in each year gives a similar picture to that obtained from the population seedlings, Kent showing a longer ear, more spikelets and, in this case, a greater total length than Irish, while spikelet length and number of florets are again greater in Irish.

Differences between years occurred in all ear length characters (total length, ear length and number of spikelets) which were higher in 1957 than in 1956. The spikelet measurements, however, were fairly constant in the two years.

Most of the ear characters showed good repeatability from year to year though usually not as high as for date of ear emergence. The order of repeatabilities derived from clonal replication between years agrees fairly well with that of the heritabilities derived from replication within a single year (table 3), suggesting that the characters show the same relative stability to environmental fluctuations between and within years.

4. HERITABILITY OF EAR CHARACTERS

Methods for the separation of genetic from environmental variation, and for its analysis into additive and non-additive components have been discussed earlier (Cooper, 1959*a*). In the present work, the

TABLE 2

Ear characters in clonal replicates of Irish and Kent ryegrass 1956 and 1957

39 plants of Irish, 32 plants of Kent

	1956 Mean	1957 Mean	Difference 1956-57	Correlation 1956-57
Total length (cm.)				
Irish	41·0	44·2	+3·2*	0·81**
Kent	43·2	47·0	+3·8***	0·52**
(Difference)	+2·2*	+2·8*		
Length of ear (cm.)				
Irish	17·7	19·9	+2·2**	0·76**
Kent	19·7	23·5	+3·8***	0·58**
(Difference)	+2·0***	+3·6***		
No. of spikelets				
Irish	19·1	21·9	+2·8 N.S.	0·61**
Kent	22·1	26·5	+4·4***	0·49**
(Difference)	+3·0***	+4·6***		
Length of empty glume (mm.)				
Irish	10·6	10·6	0·0 N.S.	0·94***
Kent	9·9	10·3	+0·4 N.S.	0·80**
(Difference)	−0·7 N.S.	−0·3 N.S.		
Length of spikelet (mm.)				
Irish	15·7	16·3	+0·6 N.S.	0·71***
Kent	14·3	15·1	+0·9 N.S.	0·61**
(Difference)	−1·4**	−1·2*		
No. of florets				
Irish	10·2	11·1	+0·9*	0·70**
Kent	9·5	10·0	+0·5 N.S.	0·69**
(Difference)	−0·7 N.S.	−1·1*		
Date of ear emergence				
Irish	10·9 May	5·1 May	−5·8***	0·93***
Kent	26·2 May	23·2 May	−3·0 N.S.	0·96**
(Difference)	+15·3***	+18·1***		

* P = 0·05-0·01
** P = 0·01-0·001
*** P < 0·001

genetic and environmental variations have been estimated from the analysis of variance of replicated clones, while the additive (*i.e.* fixable) genetic variation has been assessed from the regression of progeny means on mid-parent values. Individual records were taken on three heads from each plant, and a measure of within-plant variation or " developmental error " is available for all material.

TABLE 3

Analysis of variance components from clonal replicates, 1957

	Mean	V_G	V_B	V_{GB}	V_E	V_T	V_G/V_T	$\frac{\sqrt{V_G} \times 100}{\text{Mean}}$
Total length (cm.)								
Irish	45·1	21·05	0·77	6·00	5·93	33·75	0·62	10·2
Kent	46·5	58·81	0·60	8·58	4·01	72·00	0·81	16·5
Length of ear (cm.)								
Irish	21·0	7·90	0·06	1·40	1·57	10·93	0·72	13·4
Kent	22·6	15·87	0·09	0·77	2·83	19·56	0·80	17·7
No. of spikelets								
Irish	22·3	11·87	0·08	−0·10	5·10	16·95	0·70	15·4
Kent	25·2	10·07	0·09	1·22	4·14	15·52	0·64	12·2
Length of empty glume (mm.)								
Irish	10·1	3·42	0·06	0·02	0·93	4·39	0·77	18·2
Kent	9·8	3·63	0·01	0·38	0·65	4·67	0·77	19·5
No. of florets								
Irish	11·2	0·92	0·03	0·84	1·54	3·33	0·27	8·6
Kent	10·3	2·18	0·11	0·91	1·35	4·55	0·47	14·3
Length of spikelet (mm.)								
Irish	16·9	3·11	0·18	1·67	1·97	6·93	0·44	10·4
Kent	15·0	4·97	0·21	1·03	1·60	7·81	0·63	14·9

Specimen analysis of variance

Irish	Total length, 1957 (five replicates)			
	dF	SS	MS	
Genotypes	37	12566·3	339·63	$V_E+3V_{GB}+15V_G$
Blocks	4	446·1	111·52	$V_E+3V_{GB}+114V_B$
Genotype/block interaction	148	3543·0	23·93	V_E+3V_{GB}
Between plants	189	16555·4	87·59	
Within plants	380	2254·9	5·93	V_E
	569			

$$V_T = V_G+V_B+V_{GB}+V_E$$

(i) *Analysis of clonal replicates*

The total variation for each character has been separated into genetic variation (V_G), block variation (V_B), block/genotype interaction (V_{GB}) and within-plant variation (V_E) (table 3). This separation then estimates the heritability in the broad sense as

$$\frac{V_G}{V_G+V_B+V_{GB}+V_E}.$$

These measurements were made in 1956 and 1957 on the same clonal genotypes of Irish and Kent ryegrass. Both years and both populations gave a similar picture, but only the 1957 results are presented here. For the ear length group of measurements and length of empty glume, most of the variation is genetic, but for spikelet length and number of florets, the within-plant variation is of the same order as the genetic variation and the heritability is consequently lower. For all characters, block effects or genotype/block interactions are usually less than the within-plant variation.

TABLE 4

Heritabilities from parent/progeny regressions
Irish and Kent ryegrasses, 1957

	Irish				Kent			
	Parent mean	Progeny mean	r	b	Parent mean	Progeny mean	r	b
Total length (cm.) .	45·3	49·6	0·75***	1·06** ±0·20	48·1	51·9	0·96***	0·95*** ±0·17
Ear length (cm.) .	21·1	21·9	0·56**	0·82* ±0·26	24·0	25·0	0·83***	0·81*** ±0·16
No. of spikelets .	22·3	22·3	0·83***	0·74*** ±0·15	26·3	27·4	0·54*	0·51* ±0·23
Length of empty glume (mm.)	11·1	10·2	0·84***	0·83*** ±0·12	10·3	9·6	0·61*	0·47* ±0·18
Length of spikelet (mm.)	16·9	14·2	0·13 N.S.	0·14 N.S. ±0·28	15·0	13·0	0·62*	0·36* ±0·13
No. of florets . .	11·4	10·1	−0·10 N.S.	−0·09 N.S. ±0·21	1·02	0·94	0·51*	0·20* ±0·09
Date of ear emergence	3·7 May	29·5 April	0·88***	0·89*** ±0·11	24·7 May	22·2 May	0·98***	0·93*** ±0·08
	$n = 23$				$n = 14$			

The genetic coefficient of variation

$$\left(\frac{\sqrt{V_G} \times 100}{\text{Mean}}\right)$$

which gives a rough measure of the relative improvement to be expected under selection, shows values of 8 to 20 per cent., being greatest for length of empty glume, and least for spikelet length and number of florets.

It must be remembered, however, that these estimates derived from replicated clones refer to the total genetic variation visible in the initial population. The *additive* genetic variation, *i.e.* that which is fixable by selection, can only be estimated from breeding tests.

(ii) *Parent-progeny regression*

In the present work, the *additive* genetic variation has been estimated from the regression of the progeny mean on the mid-parent value for 23 pair-crosses of Irish and 14 of Kent ryegrass, records of parents and progeny from the same year, 1957, being used. The parents were mated at random for ear characters, so no corrections for non-random mating are necessary (Reeve, 1953).

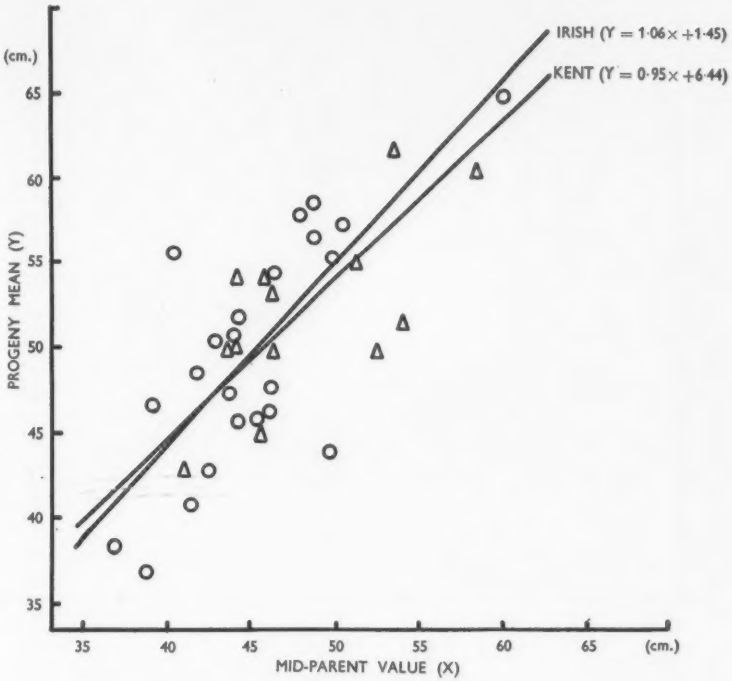

FIG. 2.—Heritability of total length in Irish and Kent perennial ryegrass. (Irish =O, Kent = △).

Table 4 gives details of the parent and progeny means, the correlations between them, and the regression of the progeny mean on the mid-parent value, while figs. 2 and 3 illustrate the behaviour of one highly heritable character (total length), and one with low heritability (number of florets).

As discussed earlier (Cooper, 1959*a*), the regression of progeny on mid-parent estimates the quantitative advance likely to be obtained under selection, while the correlation coefficient measures the deviation from linearity of the progeny values. The correlation coefficient also makes it possible to estimate heritability when parents and progeny

may differ in scale, for instance, when they are recorded in different years or in different environments.

The regression and correlation coefficients agree well for each character, and as found earlier (Cooper, 1959*a*), the date of ear emergence shows a very high heritability in both populations.

In Irish ryegrass, the ear length group of measurements, and length of the empty glume are highly heritable, while spikelet length and number of florets show little, if any, heritable variation. The order

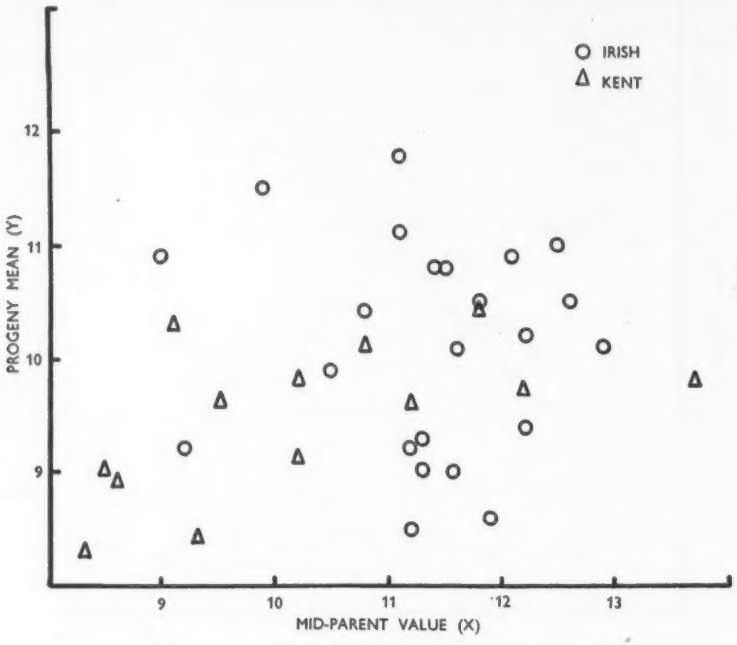

FIG. 3.—Heritability of number of florets in Irish and Kent perennial ryegrass. (Irish = O, Kent = △).

of these results agrees with those obtained from the analysis of clonal replicates.

In Kent, the situation is slightly different. Total length and ear length again show high heritabilities, but the estimates for number of spikelets and length of empty glume are somewhat lower, though still about 50 per cent. In this strain, length of spikelet and number of florets also show some heritable variation. The amount of genetic variation for a particular character can evidently differ from one population to another.

The high parent-progeny regression for most of these ear characters indicates that rapid immediate reponse to selection should be possible.

In addition, considerable genetic variation occurs within each progeny (table 8), and it is clear that most parents are highly heterozygous. As with ear emergence, this storage of genetic variation should allow of extensive long-term changes under selection.

5. CORRELATION BETWEEN CHARACTERS

Although the high additive heritability of most ear characters suggests that selection for each of them individually should prove effective, selection for two or more at the same time will be hindered if a negative correlation exists between the different criteria of selection.

TABLE 5

Phenotypic correlations between characters in seedlings of the initial populations

Kent (n=78)

	Total length	Length of ear	No. of spikelets	Length of empty glume	Length of spikelet	No. of florets	Date of ear emergence
Total length		0·07	0·46***	0·40***	0·29**	0·09	0·18
Length of ear	0·05		0·58***	0·34**	0·28**	0·05	−0·37***
No. of spikelets	0·24*	0·03		0·15	0·05	0·03	−0·11
Length of empty glume	0·12	0·12	−0·26*		0·14	0·27*	0·00
Length of spikelet	0·08	0·20	−0·26*	0·42***		0·59***	−0·03
No. of florets	0·03	0·04	−0·26*	0·24*	0·72***		−0·09
Date of ear emergence	0·04	−0·01	−0·10	0·01	−0·30**	−0·20	

Irish (n=78)

* P = 0·05-0·01
** P = 0·01-0·001
*** P < 0·001

Conversely, if these are positively correlated, the advance under selection should be accelerated.

The correlations of the ear measurements with each other and with date of ear emergence can thus be used to predict the expected correlated response to selection, and this prediction can then be checked against the responses actually obtained in the selection experiment.

(i) *Phenotypic correlations in the initial populations*

Phenotypic correlations between all the characters were calculated for the two initial populations of Irish and Kent ryegrass. The results (table 5) show a positive correlation between number of spikelets and total length in both strains, but between number of spikelets and ear

length in Kent only. There was, surprisingly, no correlation between total length and ear length in either strain. Negative correlations were obtained between number of spikelets and spikelet size (length of empty glume, length of spikelet, number of florets) in Irish but not in Kent. Length of spikelet and number of florets were highly correlated in both strains, while length of empty glume and length of spikelet were correlated in Irish but not in Kent.

There were few correlations with date of ear emergence, only length of ear in Irish and length of spikelet in Kent showing a slight negative correlation with ear emergence.

(ii) *Phenotypic and genetic correlations from clonal replicates*

The above measurements on population seedlings, however, only provide estimates of phenotypic correlations, while in predicting the correlated response to selection it is genetic correlations which are important. Both phenotypic and genetic correlations were therefore calculated for the clonal plants of Irish and Kent ryegrasses used as parents in the pair-crosses.

The genetic correlations were obtained from the following formula (Hazel, 1943):

$$r_G = \sqrt{\frac{b.A_pB_o \times b.A_oB_p}{b.A_oA_p \times b.B_oB_p}} = \sqrt{\frac{cov.A_pB_o \times cov.A_oB_p}{cov.A_oA_p \times cov.B_oB_p}}$$

where $b.A_pB_o$ represents the regression of character B in the progeny on character A in the parent, and so on. In the present work, mating was at random for ear characters, so no correction for non-random mating was necessary (Reeve, 1953). Where the two regression coefficients, or covariances, of the numerator are of opposite sign, an imaginary figure is obtained, indicating that the genetic correlation is not significantly different from zero. Similarly, where one of the regression coefficients or covariances in the denominator is zero or negative, indicating the absence of genetic variation, there can be no genetic correlation.

The phenotypic correlations derived from the clonal replicates were not always the same as those obtained from the population seedlings. Total length and ear length were highly correlated in both strains, as were length of spikelet and number of florets, but number of spikelets and ear length were correlated in Irish only. Rather surprisingly, length of spikelet and number of florets were positively correlated with ear length in Kent. There were again few significant correlations with date of ear emergence, except for total length in Irish, and spikelet length and number of florets in Kent.

The corresponding phenotypic and genetic correlations were usually of the same order and in the same direction (table 6). This is not unexpected as all the material was grown in the same field in the

same year and both block effects and block/genotype interactions were small (table 3). The most noticeable difference lies in the relation between spikelet length and number of florets in Irish. There was a high phenotypic correlation between these two characters, but since no additive genetic variation could be detected for floret number, there could be no genetic correlation. In Kent ryegrass, on the other hand,

TABLE 6

Phenotypic and genetic correlations between ear characters in clones of Irish and Kent perennial ryegrasses, 1957

Kent (n=14)

	Length	Length of ear	No. of spikelets	Length of empty glume	Length of spikelet	No. of florets	Date of ear emergence
Total length		0·78** (0·69)	0·36 (0·53)	0·09 (0·25)	0·46 (0·59)	0·26 (0·37)	0·09 (±0)
Ear length	0·65*** (0·75)		0·36 (0·24)	0·47 (0·65)	0·70** (0·49)	0·56* (0·25)	−0·09 (±0)
No. of spikelets	0·51* (0·57)	0·63** (0·58)		0·05 (±0)	−0·02 (−0·55)	−0·19 (−0·89)	0·35 (0·66)
Length of empty glume	0·22 (0·16)	0·50* (0·35)	0·05 (±0)		0·44 (0·59)	0·38 (0·22)	−0·12 (±0)
Length of spikelet	0·18 (±0)	0·27 (±0)	−0·23 (−0·626)	0·32 (±0)		0·82*** (0·93)	−0·57* (−0·59)
No. of florets	0·14 (±0)	0·24 (±0)	0·12 (±0)	0·02 (±0)	0·65*** (±0)		−0·50* (−0·33)
Date of ear emergence	0·44* (0·45)	−0·13 (±0)	0·19 (0·44)	−0·17 (−0·03)	−0·21 (−0·53)	0·07 (±0)	

Irish (n=23)

(Phenotypic correlations without brackets, genetic correlations inside brackets.)

* P = 0·05-0·01
** P = 0·01-0·001
*** P<0·001

both the genetic and phenotypic correlations between these two characters were high.

The largest genetic correlations with ear emergence in Irish ryegrass were positive for total length and number of spikelets and negative for spikelet length, while in Kent there were a positive correlation for number of spikelets, and negative for spikelet length and number of florets. One would therefore expect these characters to show a correlated response to selection for ear emergence. There were few high genetic correlations between the other measurements suggesting that most of the ear characters could be selected independently.

6. CORRELATED RESPONSE TO SELECTION

Correlated response to selection was assessed on the third generation material in 1957 by taking the early and late selection lines derived from the same initial group of parents, and determining the significance of the difference between them for each ear measurement. Ten seedlings were measured in each line. It will be recalled that early and late selection lines had been established from a number of initial groups of four, two and one plant, and that by the third generation considerable response in ear emergence had occurred within each group (Cooper, 1959*b*).

TABLE 7

Correlated responses to selection for date of ear emergence

	Irish							Kent						
	Negative response			No response	Positive response			Negative response			No response	Positive response		
	***	**	*		*	**	***	***	**	*		*	**	***
Total length	...	...	...	8	1	...	...	...	...	...	5	...	...	2
Ear length	...	...	1	6	...	1	...	1	...	...	5	...	1	...
No. of spikelets	...	...	...	7	1	...	...	...	1	...	2	...	2	2
Length of empty glume	2	2	...	4	1	...	...	1	...	1	5	...	...	...
Length of spikelet	1	2	1	5	...	...	...	2	1	1	3	...	...	...
No. of florets	...	...	2	7	...	...	...	1	...	1	5	...	...	...

(Figures refer to number of pairs of lines showing each type of response.)

* $P = 0{\cdot}05\text{-}0{\cdot}01$
** $P = 0{\cdot}01\text{-}0{\cdot}001$
*** $P < 0{\cdot}001$

A summary of the results is given in table 7 for Irish and Kent separately. There were no regular differences between the lines derived from four-way crosses, pair-crosses or selfings followed by sib-mating, and these have been bulked in the table. Most pairs of lines showed a correlated response in one or more characters but the different ear characters seemed to change quite independently of each other. In both strains, selection for lateness tends to produce an increase in the ear length characters (total length, ear length, number of spikelets) and a decrease in spikelet size (length of empty glume, spikelet length, number of florets) but the direction of response is not invariable. In Irish, for instance, one group has given a negative response for ear length and another a positive response for length of empty glume.

The changes in ear characters which occur as a result of selection for ear emergence bear no regular relation to the genetic correlations calculated from the initial material, and may well be a result of chance

TABLE 8

TABLE 8

Effect of mating systems on ear characters

	Total length (cm.)		Length of ear (cm.)		No. of spikelets		Length of empty glume (mm.)		Length of spikelet (mm.)		No. of florets		No. of families
	Means of		Means of		Means of		Means of		Means of		Means of		
	means	variances	means	variances	means	variances	means	variances	means	variances	means	variances	
(*a*) *Irish*													
Original populations	51·6	35·4	23·4	11·4	23·9	10·3	10·2	5·3	15·4	4·8	10·6	2·03	3
1st generation													
Pair crosses	48·0	20·1	21·6	10·2	22·0	7·2	11·2	3·4	14·8	1·5	10·6	1·57	4
Selfings	35·8	*	17·6	*	19·7	*	10·9	*	16·2	*	11·8	*	4
3rd generation													
Four-way crosses	48·1	28·6	21·9	10·8	22·8	5·5	9·9	2·9	14·2	3·3	10·1	2·29	4
Sib-crosses	38·5	24·7	16·3	10·2	19·5	8·4	9·5	1·5	13·4	2·6	10·3	1·44	7
Selfing/sib-crosses	38·7	22·5	19·6	7·3	22·2	8·7	10·5	2·3	13·4	1·6	10·3	1·23	6
Selfed lines	34·8	10·4	17·4	4·1	21·0	2·5	10·0	1·4	13·4	0·9	9·9	0·99	3
Developmental error													
Outbred		2·0		0·52		1·70		0·31		0·66		0·51	
2nd generation selfings		1·4		1·36		2·04		0·31		0·50		0·51	
(*b*) *Kent*													
Original populations	52·1	33·2	24·9	11·9	27·8	13·3	10·4	3·2	15·3	5·3	10·0	2·27	3
1st generation													
Pair crosses	53·2	20·2	27·1	9·9	28·9	6·3	9·7	2·1	12·7	1·7	9·3	1·01	4
Selfings	40·5	*	20·5	*	23·0	*	10·0	*	14·5	*	8·9	*	4
3rd generation													
Four-way crosses	51·3	31·0	24·1	9·8	26·1	10·7	10·0	1·1	12·8	1·2	8·9	1·11	4
Sib-crosses	51·2	41·4	23·1	9·1	26·4	15·0	9·8	1·9	12·7	2·2	9·3	0·99	5
Selfing/sib-crosses	50·6	10·7	24·9	3·5	25·1	3·9	9·2	1·1	13·4	1·7	9·2	2·07	3
Selfed lines	44·1	22·1	22·1	10·2	19·9	7·3	9·9	2·0	12·0	2·8	9·3	1·79	3
Developmental error													
Outbred		1·3		0·94		1·38		0·22		0·53		0·45	
2nd generation selfings		0·6		1·05		1·82		0·45		0·79		0·53	

* Only 4 plants from each family measured, so no variance available.

association of genes in the parents used in each generation. They may also in part result from the linkage and reassortment of genes controlling ear characters with genes for date of ear emergence (Mather and Harrison, 1949).

7. EFFECT OF MATING SYSTEM

In addition to any correlated response to selection, the means and variances of the ear characters may change as a result of the different intensities of inbreeding practised. The effect of the mating system on each ear character has therefore been assessed by averaging the means and variances of all lines under the same mating system in the same generation, *i.e.* with the same theoretical coefficient of inbreeding (table 8). These can then be compared with three different measures of outbred material, (i) the original populations, (ii) the first-generation progenies from pair-crosses, and (iii) the progenies produced by outcrossing in the third generation. The influence of inbreeding on the within-plant variation has also been assessed from clonal material of the original populations and of the selfed lines in the second generation. Since the material was randomised, and block differences were small, the significance of the difference between any two means can be roughly assessed by a "t" test; significant differences at 5 per cent. are of the order of 2-3 cm. for total length, 1-2 cm. for ear length and 1-2 for number of spikelets. The spikelet measurements show few significant differences.

Pronounced inbreeding depression is shown by the ear length characters (total length, ear length, number of spikelets), but not to any appreciable extent by the spikelet measurements (figs. 4 and 5). The four-way crosses, which were based on four unrelated parents and continued by selecting four plants in each generation, seem to maintain their vigour quite satisfactorily when compared to the three outbred standards. Sib-crossing, however, usually results in a decrease in vigour, as assessed by ear length characters, while continued selfing has an even greater effect.

A decrease in genetic variance might be expected within the selection lines as a result of the inbreeding accompanying the selection programme. For most characters, such a decrease does occur in the first generation pair-crosses, but the subsequent decrease is less than expected, except for the selfed lines in Irish ryegrass, which after three generations show greatly reduced variances for most characters although still above the level attributable to developmental error (figs. 4 and 5).

There appears to be no regular change in the "developmental error" of these ear characters accompanying inbreeding, although for length of ear and number of spikelets in both strains, and for the spikelet measurements in Kent, the second generation selfed lines show somewhat higher within-plant variances.

Both the maintenance of genetic variation under continued inbreeding, and the lack of change in the within-plant variation are

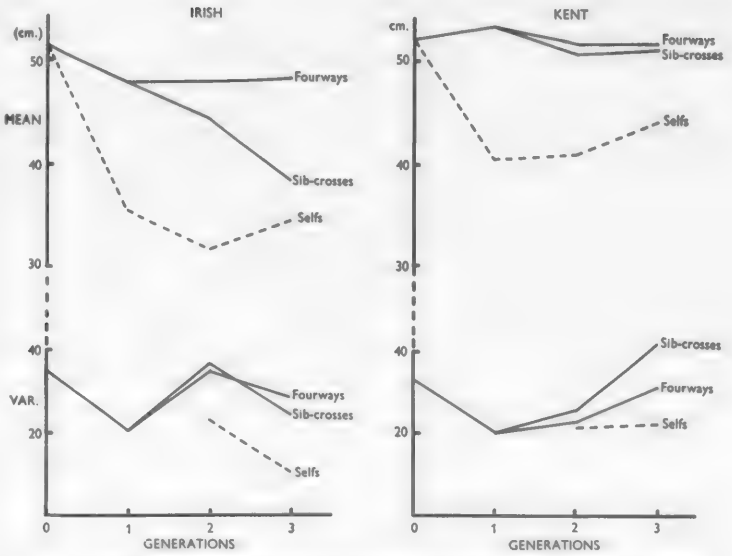

FIG. 4.—Effect of mating system on total length in Irish and Kent perennial ryegrass.

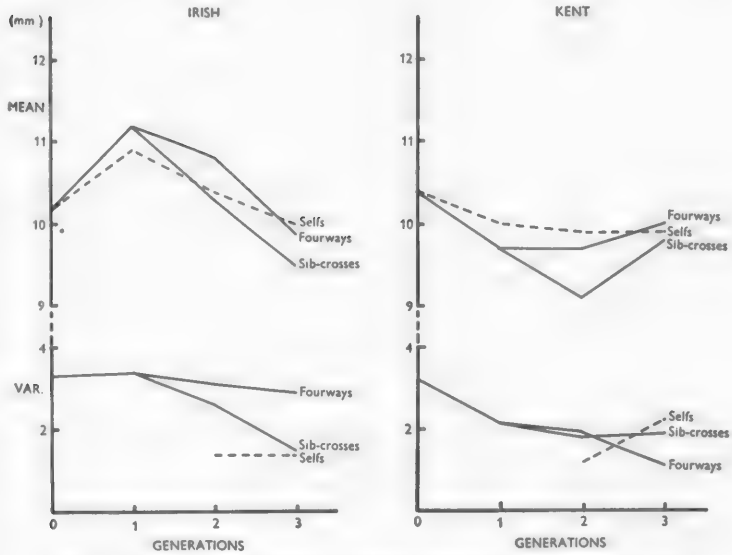

FIG. 5.—Effect of mating system on length of empty glume in Irish and Kent perennial ryegrass.

features which have been found earlier for date of ear emergence also (Cooper, 1959*b*); they may well be a result of natural selection for balanced heterozygotes during the course of the experiment.

8. DISCUSSION

The present records on the individual ear characters reveal a similar genetic structure to that shown by date of ear emergence (Cooper, 1959*b*). For most characters, considerable additive genetic variation exists in both populations, all parents are highly heterozygous, and rapid response to selection should therefore be possible, except perhaps for floret number or spikelet length in Irish ryegrass. These findings may have some practical implication in selecting for high seed yield, although Davies (1954) reports that in S23 perennial ryegrass, intrinsic seed fertility, measured as percentage seed set, is more important than number of florets per inflorescence in determining final seed yield. It is intended to measure both male and female fertility in these selection lines in later generations.

These records also provide information as to the optimum number of foundation plants on which to base a strain of ryegrass. As discussed earlier (Cooper, 1959*b*) the argument has been that too few plants might give rise to inbreeding depression during subsequent multiplication, while too many, besides being difficult for the breeder to handle, might release too much variation. The present results show that for ear characters, as for date of ear emergence, one individual carries a great deal of potential genetic variation, which can be rapidly released by segregation and recombination. Furthermore, in the four-way crosses, there has been little, if any, loss of vigour during three generations of multiplication, and little decrease in genetic variation compared to the original population. This suggests that four unrelated plants should be quite adequate as the basis of a strain of perennial ryegrass.

The correlation between the ear characters and their correlated response to selection give further information on the genetic structure of these ryegrass populations, and from the plant breeding point of view indicate possible limitations to selection for two or more characters simultaneously.

In spite of the developmental relationship of some of the characters, for instance, that between spikelet number and length of ear (Hänsel, 1951), few high genetic correlations have been obtained. There is evidently appreciable independent genetic control of these characters and it should be possible to select for them independently.

This conclusion is borne out by the pattern of correlated response to selection for date of ear emergence. As table 7 shows, although changes in ear characters have occurred in some of the selection lines, these changes are not inevitable, and are not always in the same direction for a particular character. There is, however, a tendency in both Irish and Kent for the ear length measurements to increase

and the spikelet measurements to decrease with selection for lateness of heading.

There are two possible mechanisms for correlated response to selection: (i) pleiotropic action of single genes or combinations of genes, or (ii) linkage of genes controlling different characters. In the present case, there is no high genetic correlation between date of ear emergence and any of the other ear characters, nor is there an invariable correlated response in one particular direction. Both these points seem to rule out large pleiotropic effects of single genes or gene combinations.

A more probable mechanism for these changes is the linkage of genes controlling ear characters with those controlling date of heading in the same balanced combinations. Selection for early and late date of heading will thus result in the reassortment of these genes controlling ear characters. This reassortment of linked genes as a result of selection for one particular character was first suggested by Mather and Harrison (1949) to explain the irregular pattern of correlated response to selection for high and low chaeta number in *Drosophila*.

Changes may also occur as a result of the chance association of genes in the parents selected. Clayton, Knight, Morris and Robertson (1957), for instance, working on *Drosophila melanogaster*, conclude that if the genetic correlation between two characters is low, the main source of correlated response is genetic sampling, especially in small populations. In the present work on *Lolium* the genetic correlations are low, and the chance association of genes is likely to be intensified by the small number of parents selected in each generation.

9. SUMMARY

1. A number of ear characters have been recorded in initial populations of Irish and Kent ryegrass, and in three generations of families selected for early and late ear emergence. The heritability of each character has been calculated from the analysis of clonal replicates and from parent-progeny regression, and the phenotypic and genetic correlations between the characters and their correlated response to selection have also been estimated.

2. Total length, ear length, spikelet number and length of empty glume are highly heritable in both strains, with considerable additive genetic variation. Floret number and length of spikelet show little genetic variation in Irish but more in Kent.

3. Pronounced inbreeding depression is shown by the ear length group of measurements, but not by the spikelet measurements. The four-way mating system, based on four unrelated plants, was sufficient to maintain vigour for all characters during the three generations of selection.

4. The corresponding phenotypic and genetic correlations were usually of the same order and in the same direction. There were few significant correlations between date of ear emergence and the other

ear measurements and it should be possible to select independently for most of these characters.

5. Although changes in ear characters occurred in some of the selection lines, they were not inevitable, and not always in the same direction. It is suggested that these changes result either from the chance association of genes in the parents selected in each generation or from linkage, rather than from large pleiotropic effects.

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EFFECT OF X-RAYS ON THE MUTATION OF *t*-ALLELES IN THE MOUSE

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1. INTRODUCTION

THE *t*-alleles are a long series of recessive alleles at locus *T* of the house mouse, which show a combination of unusual properties. The dominant mutant alleles *T* and T^h produce a short-tailed mouse when heterozygous with wild-type and are lethal when homozygous. All *t*-alleles when in combination with *T* produce a completely tailless mouse, and in combination with the wild-type allele a normal-tailed one. When homozygous some *t*-alleles are lethal and others are viable and result in a normal tail. Other properties found in some alleles include effects on male fertility, abnormal segregation ratios when the allele is carried in the male, and suppression of crossing-over between *T* and nearby loci (Dunn, 1954). However, the property which is of interest here is the apparent high mutation rate to new *t*-alleles which is found in stocks carrying a *t*. For lethal *t*-alleles balanced lethal lines of genotype $Tt \times Tt$ can be formed, which breed true for taillessness. Dunn and Gluecksohn-Waelsch (1953) showed that in such lines 1 in about 500 offspring is an exceptional normal-tailed animal. These normal-tailed exceptions carry a mutant *t*-allele, being heterozygotes for the original *t*-allele and the mutant. In a balanced lethal stock carrying t^1, 11 normal tails were found in 3500 offspring and in a stock carrying t^0, 4 were found in 2000 young. The spontaneous mutation rate in male gametogenesis to recessive visible alleles at 7 loci studied by Russell, Russell and Kelly (1958) and by Carter, Lyon and Phillips (1958) was 25 out of 406,343, *i.e.* an average rate for a single locus of about $0{\cdot}8 \times 10^{-5}$. Hence the observed mutation rate of *t*-alleles is of the order of 200 times that expected for a single locus.

Since *t*-alleles have properties which, in the mouse, seem peculiar to them alone, they might seem of little interest in radiation genetics. However, Dunn (1955) has shown that they are very commonly present in wild populations. Of 18 wild populations investigated 12 contained a *t*-allele, and in these 12 populations 27 out of 47 individuals tested proved to be $+t$ heterozygotes. Hence, despite their peculiarities, *t*-alleles must be considered part of the "normal" genetic make-up of the mouse and should be included in any complete study of mouse radiation genetics.

The present work is a study of the effect of X-rays on the mutation rate of *t*-alleles with two points in view. First, it was hoped to test with

the *t*-alleles the hypothesis that the frequency of radiation-induced mutation in the mouse is proportional to the spontaneous mutation rate. Secondly, if this hypothesis were supported, then radiation-induced mutation of *t*-alleles would occur with a relatively very high frequency and balanced lethal tailless lines might prove useful stocks for the study of induced mutation in the mouse.

The experiment has proved unsuccessful in its original purpose but the results have the interest of lending support to the suggestion put forward by Lyon and Phillips (1959) that " mutation " of *t*-alleles is in fact not mutation but crossing-over in an abnormal chromosome region.

2. EXPERIMENTAL METHOD

The lethal *t*-allele, t^6, which is not distinguishable from t^0 (Dunn and Gluecksohn-Schoenheimer, 1950) was used to form a balanced lethal line of genotype $T\,tf/t^6+ \times T\,tf/t^6+$, t^6 having been shown to suppress crossing-over between *T* and the linked locus of tufted, *tf*, which affects hair growth (Lyon and Phillips, 1959)

Two-month-old males of genotype $T\,tf/t^6+$ were irradiated with a dose of either 200r or 600r of X-rays (250 kV, HVL 1·2 mm. Cu ; 10 mA ; 229r/min.) to the hind part of the body and subsequently mated.

The 600r dose was chosen so that the results should be directly comparable with those of Russell, Russell and Kelly (1958). Males receiving this dose were placed with two females of similar genotype 2-3 months after irradiation and were left to breed continuously.

The 200r dose was chosen as probably the highest dose that could be given without inducing a sterile period ; it would thereby enable sperm irradiated at all stages of maturation to be studied, which was desirable in view of the possibility that there might be one particular stage of maturation at which the *t*-alleles were peculiarly sensitive. Males irradiated with 200r were placed with 3 pairs of females for 12 weeks. They were put with the first two females immediately after irradiation and left for one week, when they were moved to the next pair. Thereafter, they were moved on at weekly intervals, returning to the first two females after one week with the third pair, and so on. Contemporaneous control unirradiated males were left breeding continuously with two females.

The young sired by these males were classified for tail length and tufted fur. All non-mutant animals were tailless and non-tufted, $T\,tf/t^6+$; two types of exceptions were found : normal-tailed non-tufted and tailless tufted. All animals of both these exceptional types were kept and tested genetically for the presence of a mutant *t*-allele. The normal-tailed animals were expected to be of the genotype t^6t^m where t^m is a mutant allele ; the tailless tufted animals were apparent crossovers between t^6 and *tf* and were tested to find whether mutation of the *t*-allele had accompanied crossing-over.

3. RESULTS

The results are shown in table 1. The numbers of animals classified for tail length and for tufted fur are shown separately since the totals are very different, as a result of death of young between the times of the two classifications. The data from the 200r series have been subdivided into young sired in weeks 1-5, by sperm irradiated in maturation stages, weeks 6-7 by sperm irradiated perhaps in maturation stages and perhaps as spermatogonia, and weeks 8-12 in which sperm were definitely irradiated as spermatogonia. Very few young were sired

in weeks 6 and 7 after irradiation; this is in line with the findings of Bateman (1958).

All the exceptional animals were found to carry mutant alleles at the *t*-locus, except for the one normal-tailed animal in the control series which died when only a few days old. The mutant alleles have

TABLE 1

Types of offspring found

Dose (r)	Offspring					
	Tailless	Normal tailed	Mutation rate $\times 10^3$	Non-tufted	Tufted	Mutation rate $\times 10^3$
0 . . .	1538	1	0·65	896	2	2·23
200 (weeks 1-5) .	642	...	0	318	1	3·14
(weeks 8-12)	854	3	3·51	477	...	0
(weeks 6-7) .	37	...	■	18	...	■
600 . . .	697	2	2·86	438	1	2·28

been given the symbols t^{h2}—t^{h10}. The four tailless tufted animals were all of the genotype $Ttf/t^{hn}tf$, and of the normal-tailed animals four were of the type $t^6+/t^{hn}tf$, while the fifth carried a new kind of *t*-allele, not producing taillessness, and had the genotype $Ttf/t^{h7}+$.

4. DISCUSSION

(i) *Test of proportionality of induced and spontaneous t-allele mutation*

One aim of the experiment was to test the hypothesis that the frequency of radiation-induced mutation in the mouse is proportional to the spontaneous rate. To make this test it is necessary to work out

TABLE 2

Ratio of induced to spontaneous mutation in specific locus experiments

Spontaneous mutations	25/406,343*†
Mutation rate	$6{\cdot}15\times10^{-5}$
Mutations after 600r to spermatogonia . . .	111/119,326*
Mutation rate	$93{\cdot}02\times10^{-5}$
Ratio of 600r mutation rate to spontaneous . .	15 : 1
Ratio induced : spontaneous mutation after 600r .	14 : 1

* Russell, Russell and Kelly (1958).
† Carter, Lyon and Phillips (1958).

expected mutation rates for the present experiment on the basis that (*a*) the rate of induced *t*-allele mutation is proportional to the spontaneous mutation rate, and (*b*) for the 200r dose, that the induced mutation rate increases linearly with dose. Table 2 shows that in the specific locus experiments previously mentioned the ratio of induced to

spontaneous mutation after a dose of 600r X-rays to spermatogonia was 14 to 1. In this experiment the spontaneous mutation observed was potentially occurring in both sexes, whereas in the irradiated series only the male parent was treated. Hence a proportional increase can only be expected in that part of the mutation attributable to the male. This part is not known but it will be assumed that half the spontaneous mutation occurred in the male, and therefore the expected mutation rates shown in table 3 have been arrived at by taking half the expected proportional increases. From the table it is clear that the increases in mutation rate of *t*-alleles after radiation treatment are

TABLE 3

Ratio of induced to spontaneous mutation for t*-alleles*

Dose (r)	Mutation rate × 10^3			Ratio to spontaneous	Ratio $\frac{\text{induced}}{\text{spontaneous}}$ mutation rate	
	Tail data	Tufted data	Total		Observed	Expected
0 . . .	0·65	2·23	2·88	...	...	...
200 (weeks 8-12) .	3·51	"	3·51	1·22	0·22	2·3
600 . . .	2·86	2·28	5·14	1·79	0·79	7·0

much less than those expected, and that the data do not support the hypothesis of proportionality.

(ii) *Is* t*-allele mutation a form of crossing-over ?*

This experiment having proved negative with regard to its original purpose its main interest lies in the light it throws on the nature of *t*-allele mutation.

The suggestion that *t*-allele mutation is in fact a form of crossing-over arises from the association of this mutation with crossing-over between *t* and nearby loci. The original *t*-allele in this experiment, t^6, was carried on the same chromosome as the wild-type allele of tufted, the genotype of all animals being Tf/t^6+. The mutants, with the exception of the unusual allele t^{h7}, were combined with *tf*, the animals being either $t^6+/t^{hn}tf$ or $Tf/t^{hn}tf$. Two explanations for this finding are possible. First, that the presence of a *t*-allele has induced a mutation in the homologous chromosome, in this case the *T-tf*-carrying chromosome; and second, that the apparent mutation of *t*-alleles is in fact the result of crossing-over in an abnormal chromosome region. Earlier work on crossing-over in mice heterozygous for *t*-alleles led to the same two explanations (Lyon and Phillips, 1959). Four cross-overs were found in the region of cross-over-suppression of t^6; three carried the complementary allele *T* or +,

according to the type of heterozygote used, and one carried a *t*-allele, which was found to be a mutant allele. The measured frequency of crossing-over in the *T-tf* region among the progeny of animals carrying t^6 was 2/526. Thus, as a crossing-over hypothesis demands, the complementary cross-over types can be found and their frequency is of the same order of magnitude as that of the mutant *t*-alleles. Consequently, although neither explanation can be critically excluded, the hypothesis that *t*-allele mutation is in fact crossing-over in an abnormal chromosome region is favoured.

(iii) *Is t-allele mutation affected at all by radiation?*

If *t*-allele mutation is not true mutation then the test of proportionality of induced and spontaneous mutation is not of general application to mutation in the mouse. On the other hand it would be of interest to test whether *t*-mutation is affected at all by radiation. To test this the data from all the irradiated animals have been pooled and compared with the control data (table 4). On the basis of tail classification only

TABLE 4

Comparison of control and irradiated series for a significance test

	Tailless	Normal tailed	Non-tufted	Tufted
Control . . .	1538	1	896	2
Irradiated .	2230	5	1251	2

the observed mutation rate in the irradiated series is higher than in the controls, but when the probability of obtaining a difference as great or greater by chance was calculated using Fisher's (1954) exact method it was found to be as high as 0·22. Moreover, considering tufted classification only, the mutation rate in the irradiated series is lower than that in the controls; therefore to combine the tail and tufted data would decrease the difference between irradiated and controls. Thus, if X-radiation increases the frequency of *t*-allele mutation at all in the male mouse then the increase is too small to be detected in an experiment of the scale of the present one.

5. SUMMARY

In balanced lethal tailless lines of the house mouse, of the genotype $Tt \times Tt$, mutation to new *t*-alleles occurs with a high frequency. The effect of X-rays on this mutation was investigated. *t*-allele mutation was not especially sensitive to radiation mutagenesis; in fact, if there was any increase at all in the *t*-allele mutation rate it was too small to be detected in an experiment of this scale. The genotypes of the

mutants obtained favoured the hypothesis that *t*-allele mutation is in fact not true mutation but a form of crossing-over in an abnormal chromosome region.

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FLOWER COLOUR IN *LOCHNERA ROSEA*

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1. INTRODUCTION

In a survey of anthocyanins of tropical plants, Forsyth and Simmonds (1954) found that the flowers of periwinkle, *Lochnera* (*Vinca*) *rosea* (*L.*) Reichenb. (Apocynaceæ), contained a pigment of which the aglycone corresponded with none of the common types recognised in other plants. Later studies (Forsyth and Simmonds, 1957) showed that the anthocyanidin was trimethyl delphinidin and corresponded in its properties with hirsutidin, a pigment which has otherwise been recognised only in the Primulaceæ (Harborne, 1958). The periwinkle is widely cultivated and escaped in the tropics and is favourable material for genetical and chemical studies of pigmentation. Genetical investigations were begun in 1955 and carried on in collaboration with two post-graduate students at this institution (Waitt, 1956; Andrews, 1957). It is the purpose of this paper to report the genetical results obtained to date.

2. METHODS

Foundation stocks were obtained from local gardens and were at first vegetatively propagated by cuttings, which are easily rooted in a sand propagator. The mature plants are vigorous perennials with a potential life of several years, though often lost to the attack of root fungi or a (yet unidentified) virus. The seed is small and the young seedlings delicate ; damping-off is peculiarly troublesome in the early stages. The plants take about 10 weeks to flower under tropical conditions and thrive best under high light intensity and light watering. They can be crowded in boxes in the open and, though stunted, flower and set fruit well under these conditions.

The morphology of the flower has been described in detail by Boke (1947, 1948, 1949). The perianth consists of a long, slender tube surmounted by a flat, five-lobed limb ; the stamens are epipetalous and cohere in a cluster around the top of the sub-globular stigma, stamens and stigma both being enclosed in a swelling near the top of the corolla tube. The pollen is powdery and the flowers are easily selfed by a means of a blunt needle inserted into the top of the tube (cf. Boke, 1949). Crossing is much more difficult for it is impossible reliably to remove the stamens without also removing a large part of the corolla. Fruit matures in four to five weeks and the follicles must be watched carefully in the later stages for they reach maturity and dehisce with little external sign of change. Seed storage presents certain problems which have not yet been worked out in detail. For short periods of storage, at least, seed should be stored in open air rather than in the desiccator or refrigerator, as the following experiment shows :

	Germination per cent. after storage for	
	5 weeks	10 weeks
Laboratory . . .	77	83
Desiccator . . .	45	45
Refrigerator . . .	35	42

3. FLOWER COLOUR AND DEVELOPMENT

Pigment is virtually confined to the limb of the corolla, the tube being green or green with faint reddish streaks in the vicinity of the anthers. On the limb, colour is almost confined to the upper surface and is always most strongly developed towards the bases of the lobes, at the point of junction with the tube; at this point the centre of the flower is raised in a distinct annulus with a crater-like centre, the crest of the annulus defining the inner boundary of pigmentation more or less sharply. Pigmentation of the under surface of the corolla limb occurs only in the most strongly coloured (V and P) flowers as a faint flush on the left-hand distal margins of the lobes exposed by convolution in the bud.

TABLE 1

Flower colour phenotypes in Lochnera rosea.
Colour descriptions after Wanscher (1953); in the last column, + indicates copigmentation, o none. The phenotype given in brackets against Fr has not been identified but is presumed to exist

Phenotype	Eye colour	Lobe colour	1 per cent. HCl extract	Cop
V (violet) .	Strong purple-violet	Light violet	Purple	+
P (pink) . .	Strong violet-purple	Light violet-purple	Reddish-purple	o
E (eye) b .	Strong purple	White	Purple	+
r .	Strong reddish-purple	White	Reddish-purple	o
F (flush) b .	Strong purple	Light purple shading to white	Purple	+
(r .	Strong reddish-purple	Light reddish-purple shading to white	Reddish-purple	o)
W (white) .	Greenish white	White	...	...

The characters of the various colour forms are summarised in table 1. For easy reference, the abbreviations given on the left-hand side of the table are used throughout this paper. Flory (1944), working in the U.S.A., recognised three phenotypes which, from his descriptions and from his mention of forms in the " light pink range ", seem to correspond as follows with the types recognised here:

Flory's " Pink " = V
" Red eye " = E
" White " = W

It should be noted that colour matching by different observers of the plants used in different investigations do not always agree exactly and that attempts to correlate Flory's colour descriptions under the Ridgway system with those used here have not been successful. Probably personal idiosyncrasy and variability in the material both contribute to these discrepancies.

Though V and P phenotypes are distinct and easily classified, each is somewhat variable as to hue and intensity of colour; no attempt has been made to classify these variations. Pink flowers, though solidly coloured at opening, tend to " break " before falling, sometimes very conspicuously and always more than V flowers: the pigment fades in angular, sharply bounded patches which spread and coalesce until, when the flower withers, pigment survives only in the eye. This behaviour is perhaps connected with relative instability of non-copigmented anthocyanins. E and F flowers present some difficulty

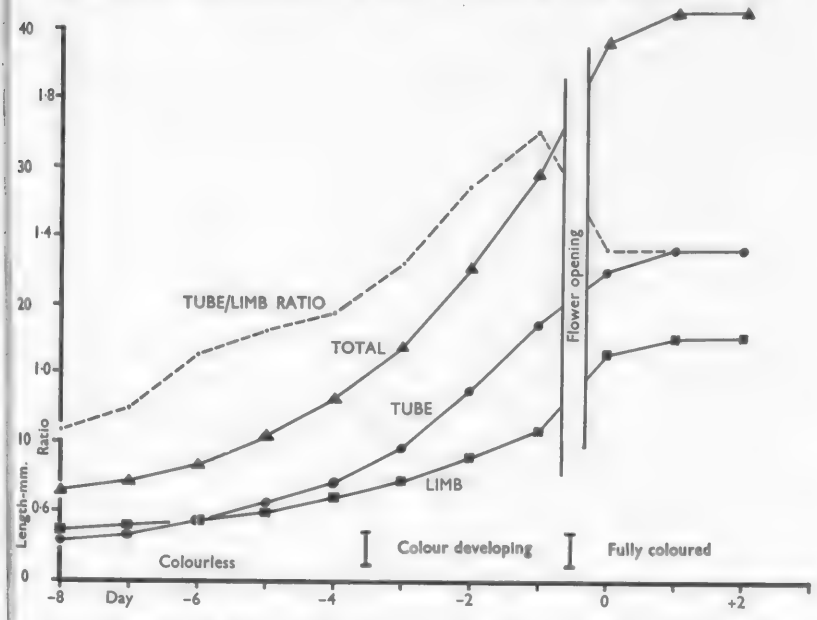

FIG. 1.—The growth of flower buds of *Lochnera rosea*. Tube and limb length (mm.) and tube/limb ratio in relation to age.

in classification, very weak flushes grading imperceptibly to the E condition.

Pink flower colour appears to be correlated with a morphological character of the flower; the annulus that encloses a crater-like depression at the eye of the flower is, in P plants, less prominent than in other phenotypes and the inner boundary of pigmentation is correspondingly less sharply defined. The result is that the eyes of P flowers are less conspicuous and pigmentation appears to be more diffuse. This character was examined in only a small minority of the families discussed here and its significance cannot yet be assessed.

At a late stage in this work, the possibility was recognised that E and F flowers are not homogeneous but contain two distinct forms,

one with pigment bluer in shade than the other. Search revealed that E plants could in fact be so classified, the bluer-toned form (Eb in table 1) owing its colour to copigmentation. All F plants seen were blue-toned (Fb in table 1) but it seems virtually certain that red-toned ones (Fr) exist and may have segregated undetected in one family described below (table 2, line 8).

In order to establish a " morphological " time scale to aid the study of colour development, flowers were tagged as young buds and daily measurements of length of tube and limb were made. Results are summarised in fig. 1 in which it will be seen that the tube grows faster than the limb up to the day of flowering, the tube/limb ratio reaching a maximum of 1·7 on the day before opening. At opening, and for one day after that, tube length continues to increase but the limb expands more rapidly and the ratio falls. Each flower lasts for two days, sometimes for three; there is no perceptible increase in size after the second day. Boke (1948, fig. 25) gives diagrams to illustrate flower development.

This established, 160 buds were measured, dissected and scored for colour development. The measurements yielded an estimate of age and the results are plotted in fig. 2. The colour scoring scale used was: 0—no pigment; 1—very faint eye colour; 2—medium eye colour; 3—strong eye colour; 4—strong eye, weak or partial lobe colour; 5—strong eye, full lobe colour. It will be seen from fig. 2 that V flowers, the most strongly pigmented at maturity, were distinctly faster to develop colour in the bud stage than other phenotypes; the least pigmented phenotype, E, was the slowest and the intermediate phenotypes, F and P, developed at a similar rate, though P finally exceeded F. All pigmented flowers, it will be noted, pass through a stage in which pigment is confined to the eye.

The chemical study of the pigments responsible for flower colour is little advanced and cannot be treated in detail here. Forsyth and Simmonds (1957) found that the bulk of the anthocyanin present was a glycoside of hirsutidin * which was accompanied by traces of glycosides of petunidin and malvidin. In P, E and F phenotypes, the hirsutidin glycoside alone has been detected (though the other two may well have been present in low concentration). Three anthoxanthins also occur in the flowers. All three were detected in the lobes and/or eyes of V, P, E and F phenotypes and there was, to judge from visual examination of chromatograms, wide variation in their absolute and relative amounts. Copigmentation was found to be responsible for the blue tones of V and Eb flowers in comparison with P and Er (table 1). Differences between the colour of fresh extracts of coloured petals in 1 per cent. aqueous hydrochloric acid corresponded with differences between the living flowers. On boiling, the bluer solutions reddened but blued again on cooling, whereas the redder solutions were unaffected.

* Strictly, of trimethyl delphinidin ; the position of the methyl groups in the *Lochnera* pigment has not been proved though it seems likely, *a priori*, that they correspond in position with those of the *Primula* anthocyanidin.

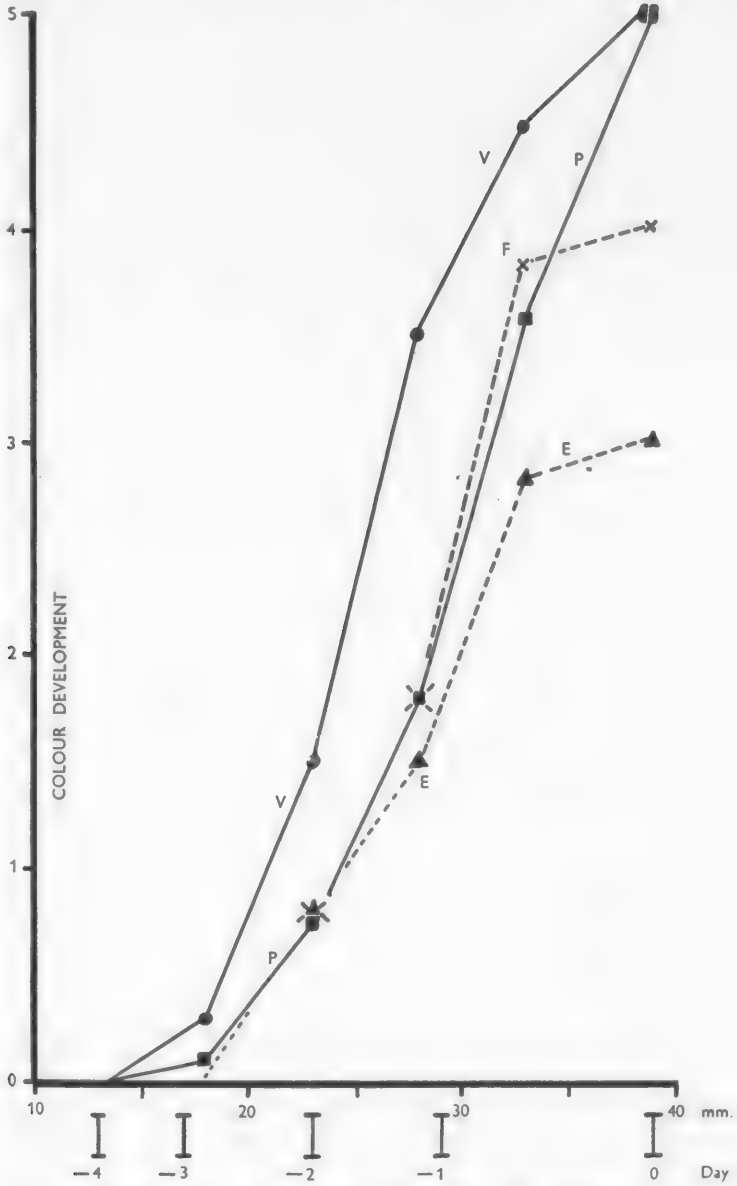

FIG. 2.—The development of colour in flowers of *Lochnera rosea*. Stages 1, 2, 3—weak, medium and strong eye colour; 4—weak limb colour; 5—strong limb colour. Horizontal scale—total bud length (mm.) with corresponding age scale (from fig. 1).

4. GENETICAL RESULTS

The stocks of periwinkle used in these experiments were probably all diploid and cytologically normal. Temporary PMC preparations in acetocarmine yielded the chromosome count, $n = 8$, in agreement with the observation of Furusato (1940). No sterile plants or plants showing *gigas* characters suggestive of polyploidy were noted in any of the cultures.

In preliminary selfings of plants isolated vegetatively from local gardens, several hundred progeny were raised. All the parents proved to be true breeding (neglecting a very few evident rogue plants). At the St Augustine Nursery of the Trinidad Department of Agriculture,

TABLE 2

Segregations for flower colour in Lochnera rosea

Parentage	F_1	Segregation in F_2 V	P	E	F	W	Heterog. χ^2 [D.f.]	Ratio tested†	χ^2 [D.f.]
1. V×P*	V	261	70	...	...	...	...	3 : 1	2·62 [1]
2. V×E	V	33	...	14	...	...	0·20 [1]	3 : 1	0·43 [1]
3. V×F*	V	62	...	2	20	...			
4. V×W (1)	V	25	...	...	...	21	...	9 : 7	0·07 [1]
5. V×W (2)	V	65	...	...	...	23	...	3 : 1	0·06 [1]
6. P×E (1)*	V	110	32	20	...	...	7·62 [2]*	9 : 3 : 4	14·37 [2]***
7. P×E (2)	V	14	1	7	...	...	3·58 [2]	9 : 3 : 4	2·99 [2]
8. P×F*	V	67	14	8	18	...		9 : 3 : 4	2·91 [2]
9. P×W*	V	135	48	...	...	51	...	9 : 3 : 4	1·44 [2]
10. E×W*	V	113	...	22	...	33	4·56 [2]	9 : 3 : 4	4·18 [2]
11. F×W*	V	157	...	18	31	69			
12. E×F*	E	...	...	83	175	...	...	81 : 175	0·03 [1]

* These families were grown in reciprocal ; all were homogeneous.

† Combining E and F classes for purpose of analysis, except in bottom line (see text).

periwinkle plants are regularly raised in large numbers for public sale. It is nursery experience that V, P, E, F and W stocks breed true year after year from open-pollinated seed (S. Bharath, personal communication). These observations, together with those of Boke (1949), make it clear that the periwinkle is fairly highly inbred.

Nineteen out of the twenty possible crosses involving five phenotypes (V, P, E, F, W) were made and F_1 and F_2 results are summarised in table 2. For the purpose of preliminary analysis, E and F classes have been combined into one (referred as E-F) since they tend to intergrade and, as will be seen in table 2, behaved in a similar fashion in combination with other phenotypes.

The only aberrant family is the cross P×E (line 6) which showed a significant deficiency of E plants. Repetition of the cross gave the results summarised in line 7; these results are heterogeneous with the preceding but agree with the results of the parallel P×F cross (line 8) and with a theoretical 9 : 3 : 4 ratio. From this F_2 (*i.e.* P×E(2)—line 7), twenty-two small F_3 families were raised, with the following results. Of the V plants, two bred true (giving 32V), three segregated pinks (21V : 7P) and nine segregated all three phenotypes (52V : 26P : 24E—$\chi^2[2]$ for 9 : 3 : 4 = 3·09); the single pink F_2 plant segregated 9P : 6E ($\chi^2[1]$ for 3 : 1 = 1·80); and the seven E plants all bred true (giving 86E). Two expected F_2 genotypes were not recovered, namely a V plant segregating 3V : 1P and a true-breeding pink. These facts all agree with the hypothesis that two genes were segregating and interacting in such a way as to give a 9 : 3 : 4 ratio in the F_2. There is no evidence of the occurrence of disturbance in segregation detected in the earlier F_2 of the same percentage. It is concluded that the aberrant F_2 family (line 6) suffered some viability disturbance that eliminated a proportion (about one-third) of the E plants.

The following scheme accounts for the main facts of colour determination in the periwinkle. The Symbols *W* and *R* are the same as those used by Flory (1944) since identity seems to be reasonably certain.

	AR			*aR*, *Ar* and *ar*
	W		*w*	
Genotype	*B* *b*		*B* *b*	
Phenotype	V P		E-F (Eb, Fb)	E-F (Er, Fr)	*W*

A and *R* are basic colour genes complementary in action.
W is concerned with pattern, W being wholly coloured, *w* limiting pigment to the eye region.
B is a copigmentation gene which blues the pigment in *W* genotypes (probably also in *ww*—see below).
W and *B* are hypostatic to *A* and *R*.

Although proof is lacking, E-F plants having been incompletely classified, it is likely that blue-toned E flowers (Eb of table 1) bear to red-toned flowers (Er) the same relation that V bears to P—*i.e.* they are copigmented by the action of *B*; this is indicated in brackets in the scheme above.

On this basis, the observed segregations are interpreted as follows:

Cross	F_1 phenotype	F_1 genotype	Loci segregating	F_2 ratio
V×P	V	*ARWBb*	*B*	3V : 1P
V×E-F	V	*ARWwB*	*W*	3V : 1E-F
V×W (1)	V	*AaRWB* or *ARrWB*	*A* or *R*	3V : 1W
(2)	V	*AaRrWB*	*AR*	9V : 7W
(3)*	V	*ARrWwB*	*RW*	9V : 3E-F : 4W
P×E-F	V	*ARWwBb*	*WB*	9V : 3P : 4E-F
P×W	V	*AaRWBb* or *ARrWBb*	*AB* or *RB*	9V : 3P : 4W
E-F×W	V	*AaRWwB* or *ARrWwB*	*AW* or *RW*	9V : 3E-F : 4W

* From Flory; other entries from the present work.

The results also suggest (though hardly prove) the nature of the genetic difference between E and F phenotypes. Flush crosses yielded in the F_2 (data from table 2):

Line	E	F
3	2	20
8	8	18
11	18	31
12	83	175

These results obviously suggest that a system of complementary dominant genes control the restriction of pigment to the eye itself. If four independent loci were concerned, the expected ratio would be 81 : 175 and the figures homogeneously agree with this ratio:

Item	χ^2	D.f.	P
Deviation (81 : 175) . .	0·095	1	0·7-0·8
Heterogeneity . . .	6·387	3	0·1-0·05

Most of the heterogeneity χ^2 is contributed by the first entry in the table, in which there is a suggestive (though non-significant) deficiency of E plants. As a working hypothesis, therefore, it seems that the F stocks used were quadruply recessive (say *lmno*) and that all the others tested were homozygous dominant at the same loci (*LMNO*).

5. CONCLUSIONS AND SUMMARY

Four major genes control flower colour in *Lochnera rosea*. Two (*A* and *R*) are basic complementary genes without both of which the flower is white. Coloured (*AR*) genotypes are modified by *W* and *B*, *ww* plants having pigment confined to the eye of the flower, *W* flowers being fully coloured; *B*, by copigmentation, blues the pigment in an *ARW* background, probably also in *ARww* genotypes. An independent system of complementary dominants controls the distribution of pigment in eyed plants, variously restricting it to the eye region alone or permitting it to spread out onto the corolla limb. The result is that five main phenotypes may be recognised (Violet, Pink, Eye, Flush and White); probably, Eye and Flush colours could be classified as blue- or red-toned, making seven distinct phenotypes in all. The predominant anthocyanin present in pigmented flowers is a glycoside of hirsutidin (but see footnote p. 256) which is accompanied by anthoxanthins. Further chemical studies are required but it is clear that variation in flower colour is procured primarily by variation in rates of development and distribution of pigment and by copigmentation rather than by chemical variation in the pigment itself. Study of colour development shows that all flowers, even fully pigmented ones, pass through an " eyed " stage. This fact, the fact that eye colour is always much stronger than limb colour and the radial streakiness of colour in E and F phenotypes jointly suggest that the eye is the primary site of pigment synthesis and that the rate of production in and spread from this centre is controlled by *W-w* and by the complementary recessives that determine the Flush character.

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Note added in proof : for a recent discussion of the botany of this plant and for good line drawings, see Lawrence, G. H. M. (1959)—*Baileya*, *7*, 113-9. Lawrence puts forward a strong argument for treating the species as a member of a genus distinct from *Vinca* under the name *Catharanthus roseus* (L.) G. Don.

POSSIBLE CASES OF AFFINITY IN COTTON

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1. INTRODUCTION

The rapid re-establishment of plants of the parental species, after interspecific crossing, is a phenomenon very familiar to cotton-breeders and geneticists. There is abundant evidence of its occurrence in a number of situations: on inbreeding interspecies hybrids, on back-crossing their progeny to either parent species, and on growing in a mixed cultivation members of interfertile species. (Stephens, 1950, is a convenient source of references.)

On Harland's theory (1933 *et seq.*), each species evolves its own " architecture " of modifier systems and dominance mechanisms, and only those segregants survive, in generations following crossing, which receive complexes approaching either parental " architecture ". This theory has been long accepted and found useful.

More recently, Stebbins (1945, 1947) has put forward the idea of " cryptic structural differentiation "; this envisages small sections of chromosomes rather than point mutations as the origin of differences between species. The idea is strongly supported by Stephens (1950), who has collected substantial cytological evidence, and some genetic evidence (1949). He takes the idea further than Stebbins, suggesting that, because of their structural differences, the paired chromosomes of species-hybrids are not completely homologous, so that crossing-over tends to produce deficient gametes and correspondingly defective or unbalanced zygotes.

While this process would favour the preservation of each chromosome as a whole, some workers doubt that it accounts for the rapid re-establishment of the parental types in the species under discussion, for cotton has a relatively high chromosome number; in the New World species there are twenty-six independent pairs which would still assort at random. Stephens' effect would be strengthened if there were also a mechanism tending to keep the chromosomes together.

Such a mechanism, in the form of the theory of " affinity ", has in fact been proposed by Michie (1953 *et seq.*) and Wallace (1953 *et seq.*), to explain certain non-random associations of individual markers (or " quasi-linkage ") in mice. It focuses on the centromere, since the function of this organelle appears to be to initiate the passage of the paired chromosomes to opposite poles at the first division of meiosis. It proposes that centromeres of the same ancestral origin tend to travel to the same pole; thus all the genes of the same origin tend to travel together—except those which are recombined with their centromeres.

Quasi-linkage has been observed not only in the F_1 of crosses between distantly related individuals in mice but also in laboratory stocks which are many generations removed from the crosses by which their several mutants were combined. Here, there is no need to call upon the selection of modifier systems or the reduced survival of defective zygotes by crossing-over within structurally differing homologues. It is clear then that affinity can operate alone; on the other hand, *if* it operates in the process of re-establishment of parental species after hybridisation, its effect would be, and very probably is, enhanced by these phenomena.

The finding of affinity in species other than mice would be of considerable interest. It is most clearly discerned as the non-random segregation of markers known to be independent; but unfortunately it does resemble linkage. Certain discriminative features are therefore noted below. (These have been considered in detail elsewhere, Wallace, 1958.)

(i) Association of markers known to be independent: recombination values may be less than 50 per cent. or more, depending on centromeric phase. Recombination in excess of 50 per cent. (reversal) is particularly discriminative since only in the case of chromatid interference can this occur in chromosomal linkage and then it is not usually expected to exceed 56 per cent. (Wright, 1947; Fisher *et al.*, 1947; Owen, 1953).

(ii) Non-linear linkage and quasi-linkage relations of segregating markers.

It is thought on theoretical grounds that the greater centromeric differentiation should occur between rather than within species. Accordingly distinctive evidence for affinity would be *the finding, on the one hand, of data exhibiting both of the features listed above in descendants of crosses between distantly related individuals* (such as species-hybrids or the F_1 of inter-varietal crosses), *and, on the other, of complete independence* (rather than "loose linkage") *of such quasi-linked markers in data from more closely related individuals* (such as members of the same species or variety or selfed line).

Sir Joseph Hutchinson has drawn my attention to a possible case of quasi-linkage in the tomato and to several in cotton. The tomato data (Sawant, 1958) is treated elsewhere (Wallace, 1960*a*). The possibility of affinity in cotton would be of particular interest to the student of evolution, for the process of speciation has probably been more thoroughly examined in this genus than in any other organism. If present, affinity must play a part; whether it is largely causative or largely a result of the process would then have to be considered.

2. THE DATA

(i) *The blackarm genes B_2 and B_3*

(*a*) *Knight's data and the linkage interpretation.* B_2 and B_3, the mimic genes for resistance to blackarm disease, were transferred by Knight (1944) from *G. punctatum* (Bar 3) to *G. barbadense* (Sakel). After the

initial outcross, repeated coupling backcrosses to *barbadense* were made, and F_2 progenies were grown from several of the backcrosses. Special repulsion backcrosses were made up, also from various coupling backcross progenies. The progenies from the early backcrosses and the F_2 progenies gave non-random assortment, and the later ones random or nearly random assortment; the repulsion data agreed according to its early or late origin. A similar programme, though less extensive, was carried out using another *punctatum* strain (Gambia Native), and similar results were obtained.

The data from the first four Bar 3 backcrosses were homogeneous and gave a recombination value of about 32 per cent., very significantly different from 50 per cent. (χ^2_1 testing independence exceeds 300). This led Knight to conclude that the genes are in fact linked. The "loss of linkage" on approaching the *barbadense* parent is also very marked: the last three backcrosses were not homogeneous and gave recombination values varying between 32 per cent. and 48 per cent. χ^2_1 testing their agreement with the earlier data is 18·27; thus there is no doubt that a change occurred at about the fifth backcross. Knight, then, logically attributes the loss to the replacement of the *punctatum* segment between B_2 and B_3 (hitherto maintained in each generation by the selection of coupling heterozygotes) by a *barbadense* one by double crossing-over. His assumption that crossing-over between homologues of different strains is inhibited has been amply supported in other contexts (Knight, 1950, pp. 242, 243, gives several instances, of which two are described in detail by Stephens, 1950, pp. 127, 128).

Knight was aware of the possibility, in using mimic genes, of obtaining linkage-like effects by other processes than linkage—linkage is, in fact, discernible in all parts of the data as departures from the ratios expected, on independence, within only two classes: resistant and susceptible. At several of the backcross stages, he therefore made up putative single-intercross matings from the phenotypes most likely to be B_2 only and B_3 only, as discerned by their grade of resistance, and in each case he obtained clearly the single-factor ratio expected; thus the co-existence of the two genes at all stages was demonstrated. Moreover, the crosses are dated, showing that the "loss of linkage" occurred in different years in different stocks. Genetic misclassification and environmental factors are thus very unlikely to account for these striking results.

However, the reality of relatively loose linkage between mimic genes with a variable expression can never be fully accepted without evidence from other loci, preferably one located between the two. Unfortunately no linkages are known for either of these genes.

This being the case, the offer of an explanation of Knight's findings in terms other than misclassification or linkage, may seem to be of academic interest only. Nonetheless the possibility of affinity is discussed below because the situation described is, apart from the accident

of mimicry, simple and of a kind peculiarly amenable to the demonstration of an affinity interpretation. It is hoped that, since transference of desirable genes from one strain or species to another has been the aim of many extensive programmes in cotton, geneticists other than the present writer may know of similar situations in published or unpublished data.

(*b*) *An affinity interpretation.* On the hypothesis that the linkage-like association between B_2 and B_3 is affinity rather than chromosomal linkage, B_2 and B_3 are situated near the centromeres of non-homologous *punctatum* chromosomes. The *barbadense* centromeres of these two chromosomes have a different centrotype, and the association between B_2 and B_3 in the early data is due to the tendency of the *punctatum* and *barbadense* centromeres to travel to opposite poles at meiosis I. The genetic constitution of the hybrid F_1 and of its *barbadense* mate may be written respectively as

$$\frac{B_2\alpha}{+\beta}\ \frac{B_3\alpha}{+\beta} \quad \text{and} \quad \frac{+\beta}{+\beta}\ \frac{+\beta}{+\beta}$$

where α are *punctatum* and β *barbadense* centromeres. The selection of B_2 B_3 progeny in each generation to make the backcross or intercross (by selfing) of the next generation ensures that the heterocentricity of the heterozygote is maintained—for the gamete $B_2\alpha$ $B_3\alpha$ results from simultaneous non-recombination between markers and centromeres and between centromeres. At some stage, however, crossing-over will occur, and this in the B_2 B_3 gamete must be, as in Knight's linkage hypothesis, double crossing-over, *i.e.*

$$\text{(i)}\ \frac{B_2\beta}{+\beta}\ \frac{B_3\beta}{+\beta}\ \text{or}\ \text{(ii)}\ \frac{B_2\alpha}{+\beta}\ \frac{B_3\beta}{+\beta}\ \text{or}\ \text{(iii)}\ \frac{B_2\beta}{+\beta}\ \frac{B_3\alpha}{+\beta}$$

$$B_2/C_2,\ B_3/C_3 \qquad B_3/C_3,\ C_2/C_3 \qquad B_2/C_2,\ C_2/C_3,$$

where C_2 is the centromere linked to B_2 and C_3 that linked to B_3. Since in all three cases at least one pair of homologues is homocentric, there will be no preferential segregation of centromeres at the first meiotic division and consequently independent assortment of B_2 and B_3 in the gametes. Double heterocentricity cannot be regained in later generations, since β centromeres only are supplied by the *barbadense* mate; the " loss of linkage " is thus permanent.

If the centrotypes of the parents of the " repulsion " heterozygotes and thus of the heterozygotes themselves are deduced in a similar manner, the fit of expectation to observation in the repulsion data is found to be as adequate as in the coupling.

It is thus apparent that the data fit an affinity explanation as well as they do one of chromosomal linkage.*

* A certain difficulty must be mentioned, but it is one which militates against both hypotheses equally. At first sight it appears from the data that the change in association occurs *abruptly* at the fifth backcross of Bar 3×Sakel and that several double-crossovers, on either theory, must be invoked simultaneously; this seems unlikely. However, a

Data which would discriminate between the two are of various kinds. For example, the linkage of a third factor to B_2 and B_3, allowing of a linear arrangement of the three genes on current interference concepts, would indicate linkage; whereas such a factor showing associations which do not allow of a linear arrangement would indicate affinity—and it might allow the location of the centromere in one pair of homologues. Again, by suitable breeding from the coupling backcrosses showing association of B_2 and B_3, repulsion heterozygotes could be made up some of which might give more than 50 per cent. recombination, thus indicating affinity.

It is interesting that there are intraspecific data showing 50 per cent. recombination (Knight, 1950, quotes "Cuany, unpublished"); this, in conjunction with the interspecific value of 32 per cent., would be taken in mice as evidence for affinity rather than of linkage. Its value in cotton, however, is open to some doubt in view of the known depression of crossing-over in interspecific data. Such depression is also found in the tomato (Sawant, 1958). If widespread, it will give rise to the paradoxical situation that it can both help and hinder the case for affinity. For, on the one hand, reduction of crossing-over from marker to centromere increases the frequency with which the marker will share the centromere's preferential assortment with other centromeres and their markers—and so it extends the range of loci capable of showing quasi-linkage; while, on the other hand, for any one case which depends solely on the disparity between quasi-linkage from interspecific data and independence from intraspecific, it provides the alternative hypothesis of loose chromosomal linkage in both sets of data. In the latter instance, the case for affinity must rest on the proposition that the observed disparity is greater than may be expected on experience of chromosomal linkage.

The disparity may be expressed as $\frac{x'}{x}$, where x' and x are the map-distances corresponding to the intraspecific recombination value, y', and the interspecific value, y, respectively. This measure is reasonable since the map-distance in a given physical segment in the interspecific heterozygotes is proportional to the number of cross-overs observed, and in the intraspecific ones, where this number is less, the proportionality presumably still applies. The transformations y' to x' and y to x must be based on a degree of interference suitable to the case under study. In the present one, the Kosambic conversion $x = \frac{1}{2}\tanh^{-1}(2y)$ is used in the absence of observations on interference because it has been found to have wide application. Choosing

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thorough analysis by the writer reveals that this difficulty is not present in the F_2 and repulsion parts of these data nor in the second series of crosses (Gambia Native × Sakel), and that, on certain plausible assumptions, a satisfactory explanation may be found where it does occur.

(from Knight, 1950) the chromosomal linkage cases in which there is the greatest disparity and thus this fraction is the *largest* we have:

	Known chromosomal linkages		Possible affinity B_2-B_3
	L-Lc_1	R_1-cl	
Recombination :			
Intraspecific, y'	29·9 per cent.	16 per cent.	45-50 per cent.
Interspecific, y	24·5 per cent.	8 per cent.	32 per cent.
Measure of disparity, $\frac{x'}{x}$	1·25	2·0	2·0 to ∞

The lowest linkage value tolerable by the independence data for B_2 and B_3 is not given, but 45 per cent. is chosen as a possibility in order to give the *smallest* disparity. In other words, in presenting the information above, the case for affinity has been made as weak as possible. Despite this, in the B_2-B_3 case the disparity is as large as, or larger than, in the others, and so affinity survives as the more plausible hypothesis.*

(*c*) *Conclusions.* Accepting affinity, it is worth considering what Knight's results imply both for the cottons used and more generally. (i) For those centromeres linked to B_2 and B_3—and for others also, if cumulative attraction is operating (see section 2*a*)—the *punctatum* variety of *hirsutum* differs from the *barbadense*. (These correspond to the $(AD)_1$ and $(AD)_2$ genomes respectively, but it cannot be deduced without further evidence, whether these statements can be applied to the whole genomes also.) (ii) In general, loose linkages based on interspecific data only, cannot be accepted as unquestionably chromosomal, particularly if the data are from heterozygotes of only one phase.

(ii) The L-Lc$_1$ linkage group

(*a*) *Hutchinson's data.* This group was established by Hutchinson (1934) while investigating the relation of the leaf-shape alleles (*L* locus). Lint-colour (Lc_1 locus) † was found to be linked with *L* with about 30 per cent. recombination (*Ibid.* p. 491). These data, which involve as many as eight strains of *G. arboreum*, are homogeneous; this situation alone makes an affinity explanation very unlikely and there has since been confirmation of linkage by the location of the marker li_d between the two (Govande, 1944).

By contrast, data involving *L* and the anthocyanin locus R_2, also from crosses within *arboreum*, while formally homogeneous, are

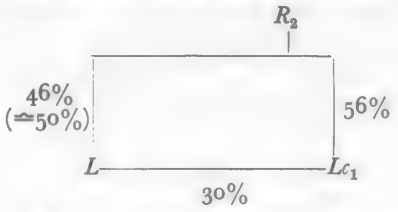
* It is impossible to devise a satisfactory test of the excess of the disparity for one case over that of another. This is because, when the intraspecific y' value expected in the case of affinity is most nearly realised, *i.e.* at or near 50 per cent., x' tends to infinity.

† The symbols suggested by Knight (1950, Appendix II) are used throughout this paper.

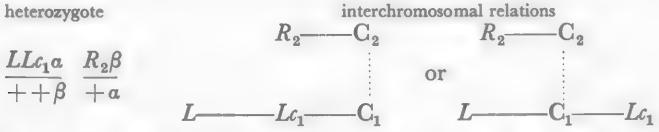
found to give rather different recombination values. Three backcrosses give, singly and together, an insignificant deviation from 50 per cent., while the fourth gives a very significant one ($\chi^2_1 = 10{\cdot}0$), the recombination value being 40 per cent. The heterozygotes in the first three backcrosses came from crosses within and between the closely related varieties *bengalense* and *burmanicum*, while the heterozygote in the fourth backcross came from a cross between the more distantly related varieties *bengalense* and *soudanense* (strain G.S.2 of *bengalense* and *Abu Hareira* of *soudanense*).

This suggests that L and R_2 are situated near different centromeres, the heterozygotes in the first three backcrosses having only one kind of centromere and thus showing independence, and that in the fourth having more than one, *i.e.* being a convergent heterocentric and thus showing the quasi-linkage. Thus at least two centromeres differ between the two strains used in the fourth cross.

So far the observations may be viewed as a typical case of affinity. However, there are further data in this paper, which, though less significant, are worth considering in view of Silow's work (section *b*), and these do not admit of so clear and single an interpretation. One of the heterozygotes in the three backcrosses described above, and a selfed heterozygote from the same source, were segregating in Lc_1 also. While the value for L-R_2 is insignificantly less than 50 per cent. (45·9 per cent.), that for R_2-Lc_1 significantly exceeds it (56 per cent., $\chi^2 > 6$). This may be represented diagrammatically:



The relations R_2-Lc_1 suggest that affinity is operating here too, this quasi-linkage being a reversal. R_2 and Lc_1 must then be near their centromeres, and these in the heterozygote are divergent. As L is linked to Lc_1 it should also show reversal with R_2. The data do admit of a value L-R_2 more than 50 per cent., but only slightly more, which indicates that the centromere of the L-Lc_1 chromosome is nearer Lc_1 than L. The situation may be represented as follows:



where C_1 is the centromere near Lc_1 and C_2 that near R_2, and each can be of the two centrotypes α and β. (The α, β designation is not, of

course, intended to imply any equivalence of centrotype with the centromeres supposedly linked to B_2 and B_3 in Knight's data.)

Before this interpretation can be accepted, two questions must be answered: (i) is the L-R_2 value in the *bengalense* × *soudanense* heterozygote, about 40 per cent., compatible with the one here which is much nearer 50 per cent.? (ii) is the supposition of two centromeres each of two centrotypes compatible with the origin of the heterozygote, mainly * from within *burmanicum*, which is so far assumed to be of only one centro-type?

On question (i): the same deviation from independence cannot, strictly, be expected unless the crosses are identical. In the present case, the *bengalense* × *soudanense* cross is known to be the wider and it is reasonable to expect the deviation from 50 per cent. to be correspondingly wider. Either or both of two factors may be responsible: depression in crossing-over between the markers and their centromeres, or increased attraction between the similar centromeres. Increased attraction may result from a *greater difference* between homologous centromeres of widely separated varieties, or from the possibility that the centromeres of *more chromosomes* are different and that they act cumulatively (Wallace, 1958, p. 219. While depression of crossing-over in cotton hybrids is well known, the idea of increased centromeric attraction has not been tested experimentally).

On question (ii): the assumption that *burmanicum* has only one kind of centromere is not strictly necessary. To explain the *soudanense* × *bengalense* result it must be postulated that those in *bengalense* are different from those in *soudanense* but this explanation is not weakened by the supposition of differences also (though smaller or involving fewer centromeres) within *burmanicum* since the strains concerned (Burma Ghost and Burma Laciniated) are morphologically very different. This supposition may, however, seem to be stretching the theory solely to accommodate a not outstandingly significant reversal. Indeed the reversal demands not only that the ancestral sources of the two chromosomes concerned have different centromeres but that there has been an interchange of these centromeres at some stage before the cross producing the divergent heterozygote. However, on hearing that the data require the postulation of an interchange, Sir Joseph has revealed that the two plants contributing the relevant chromosomes of the heterozygotes were derived from a *bulked plot* of several strains of *burmanicum* gathered from a wide range of localities in Burma, and that these plants were labelled Burma Ghost and Burma Laciniated solely on their appearance: they may well have arisen after crossing between some of these strains. Thus the means of interchange, namely crossing, is shown to have been very likely.

It must be pointed out that it is still not possible to discern, without experiment, whether or not *burmanicum* as a whole contains more than

* The pedigree given the writer shows that some contribution ultimately came from a *bengalense* plant but that it is very unlikely to have involved the chromosomes concerned here.

one kind of centromere; for it might be that interchange with other varieties has introduced new centromeres to it, rather than that the two strains of *burmanicum* concerned here have evolved differing centromeres: natural crossing between varieties whose habitats overlap, such as *burmanicum* and *bengalense*, cannot be excluded. The important point here is that quasi-linkage with an excess of recombinants should not be unexpected, and that in general, barring recent special crossing by breeders and geneticists, it may be expected in hybrids of strains, varieties or species which can cross naturally or have been able to do so in the not too remote past, *i.e.* since their divergence. The tomato data already mentioned exhibit a reversal, and here, while it is not possible to establish when the interchange occurred, the postulation of an interchange does provide an adequate explanation of several morphological and physiological relations between the varieties involved.

(*b*) *Silow's data.* Silow's data (1941) concern outcrosses of the cultivated cottons *G. herbaceum* and *G. arboreum* to the wild *G. anomalum*, and backcrosses to various strains of the cultivated cottons (not always the same species or strains in any one series of backcrosses). He established clear differences between the species at several loci, most of his data being mono-factorial. Incidental bi-factorial data, and some obtained specifically to discern linkage, are reported (*Ibid.* p. 315). All the data concern the segregation of alleles at the anthocyanin locus R_3, with those at eight other loci.

Most of the data are from late backcross generations, that is, rather too remote from the initial outcross to expect that any heterocentricity present initially can have been maintained (see section 1). Some of the data are from heterozygotes whose ancestry the writer was not able to discern very certainly from the text, but it seems likely that they were late backcrosses. Of the fifteen sets of backcross data given, most do in fact show independence, and the total ratio of non-recombinants to recombinants (pooling for all loci) shows close agreement with independence.

However, one segregation, while not deviant enough to make the total data heterogeneous, does catch the eye as showing an individually very significant departure from independence. It concerns R_3 and Lc_1: χ^2_1 is 7·2 and the recombination value 62 per cent. Inspection of the origin of the heterozygote shows that of the fifteen, this one's ancestry is the most mixed, *anomalum*, *arboreum* and *herbaceum* having all been involved. This heterozygote (the only repulsion one) may be represented as divergent in the usual way:

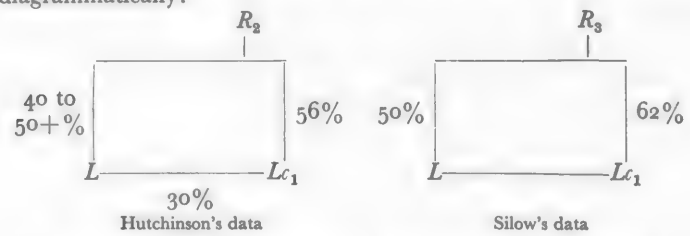
$$\frac{R_3\alpha \quad +\beta}{+\beta \quad Lc_1\alpha}$$

(Again, no identity of a centromere labelled α here with one similarly labelled elsewhere, is intended: the α centromeres are merely those which tend to travel to one pole, the β ones those that travel to the

other. Since three species have been involved in the present data, there may be three types of centromere, but there is no way of knowing from the text which are linked with each allele, and thus which show preferential tendencies.)

R_3 is not the same locus as R_2 of Hutchinson's data and they are probably in different homologues; but Lc_1 is again concerned, and again showing recombination exceeding 50 per cent. This being so, the segregation of L and R_3 is of interest: it gives independence. This could be taken as confirmation that L is farther from the centromere than Lc_1, but for the fact that it occurs in a different heterozygote where independence is probably due to partial homocentricity. One may merely observe that Lc_1 is concerned in a quasi-linkage in Silow's data as it is in Hutchinson's, but here more significantly. This is, then, confirmatory evidence for affinity.

However, as is to be expected from experiments not designed specifically to test it, affinity is not the only interpretation for both bodies of data. The observed relations between L-Lc_1 and R_2 and between L-Lc_1 and R_3, are rather similar and may be summarised diagrammatically:



On the assumption of chromatid interference, R_2-Lc_1 and R_3-Lc_1 could be chromosomal linkages. The L-Lc_1 group then becomes R_2-L-Lc_1 and R_3-L-Lc_1. However, *both* of these situations cannot be true since R_2 and R_3 are not allelic nor closely linked, so that affinity may be accepted for at least one of them. A discriminating experiment for the R_2-L-Lc_1 trio is being planned by Mr J. H. Saunders at Shambat, Khartoum.

It is hoped that those more conversant with cotton genetics than the writer may know of other cases, published or otherwise, which fit an affinity interpretation. In the present case, independence data, or data showing less than 50 per cent. recombination, for the L-Lc_1 group and either R_2 or R_3, would, according to its origin, throw light on the real nature of their relationship.

Since an experiment will usually be necessary in order to test suggestive cases of affinity, it may be useful here to outline two kinds which can probably be carried out in cotton without much preparation. (This subject has been considered in some detail elsewhere, Wallace, 1958.) Both involve the outcross of widely separated strains, varieties or species, to produce hybrids heterozygous for several factors, and both

require that these be backcrossed to a multiple recessive stock (which need have no special relation with the parental stocks).

In one kind—which is suitable for the R_2-L-Lc_1 situation—the hybrid contains at least one pair of linked factors and one or more factors not linked with these: they are chosen, if possible, on evidence such as has been described here, as being centromere markers. If their joint segregation gives linkage and quasi-linkage relations which do not allow of a linear relation between the markers, not only is an affinity hypothesis indicated but the position of the centromere relative to the two linked markers may be determined—or, if more than one pair of linked markers shows quasi-linkage, the position of the centromere relative to each pair may be determined.

In the second kind, the hybrids are heterozygous for as many independent markers as possible. If their joint segregation gives quasi-linkages, these not only identify centromere markers but supply information on centromeric differences, and possibly upon interchanges, between the strains or species used. If no quasi-linkages are obtained from interspecific data, then either (i) the markers used are not sufficiently near their centromeres, or (ii) the centromeres of the two strains or species used are the same, or (iii) the case for affinity in cotton is weakened. All these possibilities are of obvious interest. The results of this kind of experiment in mice, using differing inbred strains, are given elsewhere (Wallace, 1960*b*).

(*c*) *Conclusions.* If the relation between L and R_2 in Hutchinson's data is accepted as affinity, then

(i) these loci are near their centromeres and there are centromere differences within *arboreum*, viz., between the varieties *bengalense* and *soudanense*.

If the (less significant) relation between Lc_1 and R_2 in the same data is also accepted as affinity, then

(ii) Lc_1 is probably nearer its centromere than is L, and there may be centromeric differences within *burmanicum*.

Accepting affinity in Silow's data,

(iii) R_3 is near its centromere and there are centromeric differences between *anomalum* and either or both of *herbaceum* and *arboreum*.

These conclusions also imply

(iv) linkage group 1 (L-Lc_1) is in a different chromosome from groups 7 (R_2) and 6 (R_3).

Acknowledgment.—It is a pleasure to record my debt to Sir Joseph Hutchinson for drawing my attention to the existence of cotton data capable of an affinity interpretation, and for several fruitful discussions.

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A POSSIBLE CASE OF AFFINITY IN TOMATOES

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1. INTRODUCTION

EVIDENCE for the existence of the new genetic phenomenon, affinity, is now fairly extensive (Michie, 1955*a*, *b*; Wallace, 1958*a*, *b*, 1960*b*; Chatterley, 1958; Parsons, 1959). This has so far been entirely confined to the house mouse. Its occurrence in other species, particularly in plants rather than in animals, would be of considerable genetic and evolutionary interest.

Sir Joseph Hutchinson has drawn my attention to the existence of what appear to be significant quasi-linkages in cotton and in the tomato. It seems worth considering these, therefore, in the light of an affinity hypothesis. An analysis of the tomato data (Sawant, 1958) is the subject of this paper, the cotton data, which are rather more extensive, being treated elsewhere (Wallace, 1960*a*).

2. THEORETICAL CONSIDERATIONS

First, a brief account of the place of quasi-linkage in affinity is relevant. The theory of affinity supposes that more than one kind of centromere is possible and that two (or more) may be present in the F_1 of crosses between distantly related stocks, varieties or species. When this is the case, the centromeres of like kind, that is, supposedly from the same ancestral origin, tend to travel to the same pole at the first division of meiosis. Genetic markers linked to the centromeres then tend to be associated, that is to show quasi-linkage. The recombination values have so far been of the order of 40 to 45 per cent. Work with laboratory stocks from several countries has shown (Wallace, 1958*a*, etc.) that recombination values in excess of 50 per cent. (or reversals) are possible and have been obtained; they result from the attraction of like centromeres which have come from different parents, *i.e.* from divergent heterocentric heterozygotes.

The recombination values obtained from reversals have been in the order of 55 to 60 per cent.; as such they constitute a feature strikingly different from linkage.*

It is clear, then, that the situation most susceptible of an affinity interpretation is one where markers, which behave as if independent within the stock or species, show quasi-linkage when segregating in a

* Barring chromatid interference; this may usually be expected to produce values not in excess of 56 per cent. (Wright, 1947, and Fisher, Lyon and Owen, 1947).

heterozygote from a cross between two stocks or species; this is particularly so when the quasi-linkage value exceeds 50 per cent.

Sawant's data exhibit precisely this situation.

3. THE DATA

During a study of the phylogenetic relations of a stock of *L. esculentum* Mill. and two forms of *L. hirsutum* Humb. Bonpl., Sawant obtained *a c*/++ and *sp* ms_2/++ hybrids, which were selfed and backcrossed to the multiple recessive. The mutants were obtained in each case from the *esculentum* parent, *a* and *c* from the San Marzano variety and *sp* and ms_2 from the Pearson variety. There were two types of hybrid of each coupling heterozygote, one having its ++ contribution from

TABLE 1

Quasi-linkage of independent markers in hybrids of L. esculentum × L. hirsutum

Mating type *	Origin of *hirsutum* chromosomes	Phenotypes of progeny				Contingency χ^2 for 1 d.f.	p	Recombination value per cent.
I. *a* (V) and *c* (IV)		++	*a*+	+*c*	*ac*			
B.c. . .	Baños	171	157	136	186	5·99	0·02-0·01	45·1
I.c . .	Baños	304	110	114	37	0·15	0·7-0·5	51·5
B.c. . .	Chillon	165	158	117	172	6·47	0·02-0·01	44·9
II. *sp* (IV) and ms_2 (I)		++	*sp*+	+ms_2	*sp* ms_2			
B.c. . .	Baños	45	97	40	47	4·12	0·05-0·02	57·5
I.c. . .	Baños	67	44	24	9	1·18	0·3-0·2	58·2
B.c. . .	Chillon	140	182	127	142	0·68	0·5-0·3	51·9

* All data are coupling. B.c. = Backcross, I.c. = Intercross.

In I : χ^2_1 testing difference in recombination between Baños I.c. and Baños B.c. is 2·91, $p = 0{\cdot}1\text{-}0{\cdot}05$.

In II : χ^2_1 testing difference in recombination between combined Baños and Chillon is 2·45, $p = 0{\cdot}2\text{-}0{\cdot}1$.

the Baños stock of *hirsutum* and one having it from the Chillon stock of *hirsutum*.

Genes *a*, *c*, *sp* and ms_2 are anthocyaninless, potato leaf, self-pruning and male-sterile respectively. Sawant observes that " Genes *a* and *c* are definitely known to be located on different chromosomes (Butler, 1952) ". Rick and Butler (1956) place them in linkage groups V and IV respectively, with *sp* and ms_2 in IV and I respectively. I and V are long, well-marked groups, and *sp* is centrally placed in IV, so that independence between *a* and *c* and between *sp* and ms_2 seems pretty certain.

The quasi-linkage data are summarised in table 1.

Sawant states that the assortment of *a* with *c* and of *sp* with ms_2 " is not normal ", and that for the latter two loci, his observations

" contradict the now classical hypothesis that recombination classes in species crosses tend to be deficient and parental classes excessive ". His analysis, however, while showing that the segregations show an overall deviation from expectation, is clearly not intended to discriminate critically between disturbances due to single-factor deviations (which occur in some parts of the data) and those due to the sort of non-independence usually ascribed to linkage and now familiar in mice as quasi-linkage. A new analysis is therefore presented in the table.

4. THE ANALYSIS

Four bodies of backcross data have been pooled, after a test of homogeneity, to give the $a\,c/++$ Baños backcross progeny figures, and four also to give the Baños intercross ones. The contingency χ^2 (with Yates' correction) has been used throughout as this tests association whether or no there are single-factor deficiencies. In data where the single-factor ratios are insignificantly disturbed, the addition method of estimating the recombination value has been used, and where they are both significantly disturbed, the product method; in the intercross data, Fisher's scoring method has been used. The χ^2 tests used in the last column are based on variances which take into account possible disturbances due to single-factor anomalies.

This analysis shows that for the *a* and *c* loci there is significant association in both the Baños and Chillon hybrids. Since the data are all in one phase (coupling) there is no way of knowing whether this is quasi-linkage or interaction (in the statistical sense) in terms of preferential fertilisation, preferential pollen abortion, or zygotic inviability. Interaction of this sort, however, seems unlikely, since it has not been reported in the tomato and indeed is unusual in any species. Pollen abortion in hybrids is common but Sawant has shown that it does not explain the anomalies of any part of his data.

The paper includes data for the linked genes *Wo* and *d* (linkage group I), where the most likely explanation of the significant deficiency of recombinants in the *esculentum* × Chillon hybrid is shown to be a reduction in chiasma frequency. This is interesting: Sawant's cytological work shows that such a reduction occurs in chromosomes other than that corresponding to linkage group I. This being so, a tightening of linkage from marker to centromere is to be expected, and this, in turn, given centromeric attraction, must increase the overall degree of quasi-linkage of the markers. Sawant's cytological work, then, gives a mechanism whereby the effect of affinity, if operating, is expected to be enhanced. It is interesting to note that in cotton a tightening of linkage after interspecific crossing is commonly found, and there is now suggestive evidence that quasi-linkage also occurs after interspecific crossing.

The idea of interaction becomes even less plausible on consideration of the sp-ms_2 segregations. For one might reasonably suppose that interaction of any kind resulting from interspecific crossing would

always tend to preserve the (presumably adaptive) parental phenotypes. For the *sp* and ms_2 loci, however, as Sawant points out, it is the parental phenotypes which are deficient. In terms of linkage, the recombination value significantly exceeds 50 per cent., at least in the Baños hybrids, and thus the data exhibit this very distinctive feature of affinity. The homogeneity of each of the four bodies of data which contribute to the Baños *a-c* segregations is also encouraging. In short, both two-point segregations support the affinity hypothesis, and one shows a reversal, a feature peculiar to it.

5. DISCUSSION

While it is hardly to be expected that data from experiments not designed to demonstrate affinity can be conclusively convincing, it is worth considering what its acceptance here implies for the centromeric constitutions of the stocks involved.

For the chromosomes corresponding to groups V and IV the Baños and Chillon hybrids may be conventionally written as:

V	IV	linkage groups
$+\alpha$	$+\alpha$	*hirsutum* chromosomes (Baños and Chillon)
$a\beta$	$c\beta$	*esculentum* chromosomes (San Marzano)

where β are the *esculentum* centromeres, and α the *hirsutum*. This notation is not intended to imply that the Baños centromeres are the same as those of the Chillon, for the data do not reveal this, merely that in both hybrids a Baños centromere tends to choose another Baños one as companion in travelling to the pole, and similarly for the Chillon one. If the other ten chromosomes are also heterocentric, and if attraction between any two similar centromeres is enhanced by attraction for similar ones in other chromosomes (Wallace, 1958*a*, p. 219), then the quasi-linkage of 45 per cent. is a product of this cumulative attraction. If the data had included centromere markers for other chromosomes, it might have been informative on this point: as it stands, one may merely conclude that for two, possibly more, chromosomes the San Marzano *esculentum* centromeres differ from those of both stocks of *hirsutum*.

For the IV and I chromosomes, the Baños hybrid is a divergent heterocentric and may be written

IV	I		IV	I	
$+\beta$	$+\alpha$		$+\alpha$	$+\beta$	*hirsutum* chromosomes (Baños)
$sp\ \alpha$	$ms_2\ \beta$	or	$sp\ \beta$	$ms_2\ \alpha$	*esculentum* chromosomes (Pearson)

An alternative notation is given because these data alone do not reveal whether it is the group IV centromeres or the group I ones which have been interchanged. The important point is that there has been an interchange, for the centromeres which attract (α to α and β to β) come from different parents. Again, there may be a cumulative effect from heterocentricity of other chromosomes, and these may

also include some interchanges, but the data do not reveal this; one may merely conclude that for these two chromosomes the *esculentum* and Baños centromeres differ and that an interchange of centromeres for at least one chromosome has taken place.*

Since *c* and *sp* are both in group IV, the next logical step is to write the Baños and *esculentum* chromosomes as follows:

V	IV	I	
$\frac{+\alpha}{a\ \beta}$	$\frac{++\alpha}{c\ sp\ \beta}$	$\frac{+\ \beta}{ms_2\ \alpha}$	*hirsutum* chromosomes (Baños) *esculentum* chromosomes (San Marzano & Pearson)

That is, assuming only two types of centromere, one of the alternative notations above is impossible and one must conclude that it is the group I centromeres which have been interchanged. This interpretation may well be correct, but there is a difficulty which must be mentioned. The *esculentum* parents used in the *a-c* crosses were from a different stock (San Marzano) from those used in the *sp-ms*$_2$ crosses (Pearson), so that differing centrotypes are possible. However, though the two stocks may have been separated for more than 100 years, their appearance is closely similar, apart from the mutants, and the breeding relationship between them is as good as within either of them (Sawant, private communication). The assumption of the same centrotype is thus reasonable.

The Baños and Chillon stocks are also likely each to be homogeneous, for they are widely separated geographically and have distinct habitats and ecological niches (though Chillon is self-incompatible and so may be less homogeneous than Baños). On the assumption of homogeneity within *esculentum* and the two *hirsutum* stocks, the Chillon hybrids' centrotypes may be specified by the same sort of reasoning. Their data do not disagree with those of Baños ($\chi^2 = 2{\cdot}4527$, see table. This χ^2 takes into account the variances of *both* the Baños and the Chillon estimates of recombination). One is tempted therefore to write the three Chillon chromosomes in the same way. This implies that the same interchange has occurred in both *hirsutum* stocks and that they are thus similarly related to the *esculentum*. However, the Chillon data do agree well with independence and they do not tolerate a quasi-linkage value of the order of the Baños one (χ^2_1 is 7·9844. This takes into account the variance of the Baños estimate only; the Chillon estimate in both cases is taken from the intercross and backcross data combined). It could be argued that the data are not extensive enough to show significance beyond the χ^2 of 2·4527 just mentioned—that in fact the discrepancy may be real and is therefore worth considering further. Taken at its face value, then, the Chillon data show no quasi-linkage: the group I chromosomes are then homocentric, that is both α or both β, and thus

* Strictly, the data indicate merely that the centromere linked to *sp* attracts the one linked to non-*ms*$_2$ more than it does the one linked to *ms*$_2$ (or *vice versa* starting with *ms*$_2$); this is conceivably possible if three, or even four types of centromere were involved. But the simpler hypothesis seems preferable and is used by the present writer until proved false.

either the Chillon or the *esculentum* stock contains only one kind of centromere. Since the Baños hybrids indicate that the *esculentum* stock does in fact contain two, it is the Chillon stock which contains only one (all α).

The interesting point here is that an interchange of centromeres has taken place between Baños and *esculentum*, and that it may not have taken place between Chillon and *esculentum*. An interchange implies the probability of interchanges of other centromeres also and, more important from the standpoint of appearance and behaviour, of interchange of the genetic material of several chromosomes. This should result in greater similarity between stocks containing interchanged material than those which do not. It is striking that this is precisely the conclusion concerning the Baños and Chillon forms reached by Sawant from other considerations: the crossability, fertility, linkage relations, chiasma frequency and pollen abortion rates within these stocks and the hybrids indicate that "Baños is more closely related to *esculentum* than is Chillon". It is Sawant's view (private communication) that there has been no crossing between Baños and Chillon nor between these two and *esculentum* in the recent past. He does, however, believe it to have been possible at some time for Baños and *esculentum*, the two for which the present data give the strongest case of centromere interchange, for he has postulated it (1956) in support of a theory of semi-lethal complementary factors as a mechanism of isolation between them. It would be interesting to discover at what distant date such interchange can in fact be excluded, since this would give a minimum for the length of time the differing centromeres within each of these stocks have maintained their differences. Perhaps other tomato geneticists can supply evidence for or against the writer's speculation that the crossing took place in Europe in the early days of cultivation of this plant.

6. PAST AND FUTURE DATA

The conclusions possible in the light of the affinity hypothesis have been treated in detail because they indicate the kind of information that affinity data can supply. The treatment serves as a pointer both to the type of work that could be informative in future and to the sort of scrutiny to which past data may be subjected.

The design of affinity experiments has been dealt with in some detail elsewhere (Wallace, 1958*a*), but two points are worth emphasising here:

(i) If the four factors had been segregating simultaneously in each hybrid, the doubts mentioned above could have been avoided and the conclusions about the Chillon and Baños relations made with more certainty. Moreover, the centromere in the doubly marked chromosome (group IV) could have been mapped in relation to these markers. It is interesting to note that the only one in which centromere position

in relation to markers is already approximately known by a cytogenetic method is chromosome 2 (group I). An appropriate affinity experiment could serve as a test of this method and of the affinity hypothesis.

(ii) Evidence of quasi-linkage is critical evidence that the markers involved are on different chromosomes; it is worth more than independence data for these leave open the possibility of the markers being far apart on the same chromosome.

The situations described in this paper are very similar to those observed in mice for the genes *ru* (ruby) and *je* (jerker) (Wallace, 1958*b*), where all the " linkage " data come from outcrossed material and a " control " is provided by the occurrence of " independence " data from inbred material.

Concerning past data, it is possible that those more conversant with tomato genetics than the present writer may recall records which can be interpreted in a similar manner to those presented here.

Indeed some information of these kinds is already available. Rick and Butler (1956) state that Fogle and Currence (1950) and Butler (1951 and 1952) found evidence of linkage between *j* (V) and *wt* (X), but the trisomic tests by Rick and Barton (1954) prove their independence. The data of Fogle and Currence are stated to have occurred after a cross between " two dissimilar varieties ". This suggests that these data concern quasi-linkage rather than linkage and consequently that V and X are thereby proved independent.

On receiving a draft of this paper, Professor L. Butler, University of Toronto, has given the writer further information which is used below. His data quoted above were also from outbred material, being from the F_1 of crosses between Rouge Naine Hative (or its immediate derivatives) and other American varieties. Thus *all* the " linkage " data is from outbred material and there is strong evidence that different homologues are involved. Rouge Naine Hative was isolated from the main line of development of the American varieties almost long enough to have become a distinct subspecies (nearly 200 years), and Butler found it to be his most homozygous commercial type: it is therefore reasonable to suppose that it has developed centromeres foreign to many other varieties, and it is thus also an obvious choice for future affinity work.

It is interesting to note that in his 1951 report Butler gives an analysis of the segregation of *wt* with *f, a, lf, j*, not all, however, simultaneously (the latter linked in this order), from which an approximate idea of centromere position in V may be gained. *wt-j* and *wt-lf* have the greatest deviations from 50 per cent. (and the very significant χ^2_1 values of 83·89 and 98·91), *wt-f* less and *wt-a* none: this is consistent with a centromere close to *lf* and *j* (and of course another close to *wt* in X), but further experiment could determine the exact position.

At the Xth International Genetics Congress at Montreal, Butler commented on the *wt-j* quasi-linkage and made the following further

comments, which he has conveyed to the writer with permission to quote:

"1. When a new recessive mutant is crossed with a multiple tester stock it often gives cross-over values in the low forties with several independent markers. These 'false' linkages often disappear when the F_2 coupling test is used.

2. Crosses between *L. esculentum* and *L. pimpinellifolium*, which are perfectly interfertile, show linkages of 48 and 52 when great numbers are grown in F_2's."

These observations also support the existence of quasi-linkage and are susceptible of an affinity interpretation; but since the data were not derived in such a way that it could be the only interpretation, a direct experiment is being planned by T. Pickup, using the two latter species.

Indeed it has been the purpose of this paper to make a case for experiment both to test the reality of affinity in the tomato and to provide material from which may be extracted the information it can give on chromosome mapping and species relations.

7. SUMMARY

Sawant's data (1958), which concern the segregation of two pairs of independent markers in the hybrids of two species-crosses, are analysed in order to detect quasi-linkage.

Genes *a* (linkage group V) and *c* (linkage group IV) are found to recombine with values significantly below 50 per cent.; genes *sp* (linkage group IV) and ms_2 (linkage group I) are found to recombine with a value significantly exceeding 50 per cent. in hybrids from one cross and with a value insignificantly exceeding 50 per cent. in hybrids from the other.

The data are considered in the light of an affinity interpretation. While they are not as extensive as is desirable for a conclusive demonstration of affinity, they fit the hypothesis well.

Assuming affinity, and only two types of centromere, the genetic constitution of the chromosomes corresponding to these three linkage groups may be written:

V	IV	I	Stock from which chromosomes obtained	Origin of stock
$a\ \beta$	$c\ sp\ \beta$	ms_2 □	*L. esculentum*	San Marzano and Pearson
$+\ \alpha$	$+\ +\ \alpha$	$+\ \beta$	*L. hirsutum*	Baños
$+\ \alpha$	$+\ +\ \alpha$	$+$ □	*L. hirsutum*	Chillon

where α are centromeres of *hirsutum* ancestry, and β are centromeres of *esculentum* ancestry.

The presence of a centromere of *esculentum* ancestry in the Baños stock and one of *hirsutum* ancestry in the *esculentum* can most simply be explained on the supposition that an interchange of genetical

material (by crossing) has taken place since differentiation of the centromeres occurred.

Interchange can be expected to result in greater morphological similarity between these two stocks than between the Chillon and *esculentum* (between which it is possible that no such exchange has occurred). This expected result coincides with the conclusions drawn by Sawant from morphological, physiological and cytogenetical considerations, namely that " Baños is more closely related to *L. esculentum* than is Chillon ".

The relations between groups V and X are briefly discussed ; affinity is found to reconcile the paradox that some data show linkage between them and others independence.

An outline is given of the design of experiments to test the affinity hypothesis.

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THE EFFECT OF SELECTION ON THE MANIFOLD EXPRESSION OF THE "SUPPRESSED LATERAL" GENE IN THE TOMATO

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1. INTRODUCTION

MUTATIONS causing manifold phenotypic effects are well known and have been extensively studied (Dobzhansky, 1927; Grüneberg, 1938). They are frequently encountered in selection work on plants and animals, and, during the initial phase of selection, one seldom finds that all the character modifications that are associated with a given mutation are desirable in relation to the set objectives of selection. When apparently disconnected genetic effects can be related directly to homology of organs in development, the limits of function of a particular gene and its interaction with others are capable of more precise definition. Unfortunately this is rarely possible and in practice the finer ramifications of biochemical gene action defy recognition (Caspari, 1952). In this respect the *ls* gene in the tomato which forms the basis of the present investigation has certain advantages in that many of its manifold effects, including those which are strictly quantitative in nature, are likely to be the result of a single error in gene function which expresses itself at various stages in development. In other words the manifold effects of the mutation are probably the result of "spurious" pleiotropism (Grüneberg, 1938). Thus the conclusions from the genetic data presented later have to be considered in the light of the likelihood that most of the phenotypic modifications associated with *ls* could result from an error in a single process of growth.

The manifold effects of major gene loci can be explained either on the basis of very close linkage of genetic units with somewhat dissimilar function, or on the basis of pleiotropy. Where the linkage is very close unambiguous genetic tests to discriminate between the two possibilities are not possible in higher plants and animals and in such cases it is idle to pursue the distinction. Where correlated characters are governed by a linkage that allows a reasonable rate of recombination, the problem of eliminating undesirable associations can be solved by breaking down and reforming the linkage system. Thus it is only the region of the chromosome bearing the linkage that has to be considered and provided the homologous chromosome gives an opportunity for recombination within the region, the constitution of the rest of the genotype is of little consequence. If, on the other hand, some form of pleiotropy is involved the entire gene background becomes of primary importance in reshaping character associations. Advances under selection will then

depend on diversity throughout the whole chromosome complement and on the capacity of the gene background to modify the various character expressions independently of one another.

The independent modification by selection of the manifold effects of certain eye colour mutants in *Drosophila* was demonstrated by Dobzhansky (*loc. cit.*). As a result of outcrossing, lines were isolated having the mutant eye colours *yw* and w^i but which were wild-type in respect of spermatheca shape. The reassortment of the pleiotropic effects of the mutants was interpreted on the basis of the differential modifier effects of the gene background. Furthermore, the dominance relationships of multiple alleles at loci with manifold effects suggest that the various phenotypic expressions of a single locus may interact differently with a given gene background. This is very adequately demonstrated by the three allelomorphs *W*, W^v and + in the mouse (Grüneberg, 1942). When the effect of all combinations of the three alleles on fur colour and on macrocytic anæmia is considered, it is found that no one serial arrangement of dominance expression will fit. For example, *WW* mice have white fur and severe anæmia, while *W*+ animals develop white spotting but are free from anæmia. A somewhat similar situation is shown by the mutant gene *Ri* in *Œnothera* (Weidner, 1950). The non-seriality of the dominance effects of alleles with respect to the component expressions of pleiotropic genes provides clear evidence that manifold expressions can respond independently to the influence of modifiers.

Probably the most direct line of enquiry into the problems raised here is to study the nature of the character associations that prevail at the time of origin of major mutations (Dobzhansky and Holz, 1943). Correlated characters that are based on linkage can be expected to show character expression in the direction of the preceding selective trends. If it is therefore found that the quantitative character with which a major mutation is associated at the time of its origin shows an expression in a direction opposite to the selective pressure, one must conclude either that the mutation covered a large chromosome region in the manner of a deletion or of an inversion with extended position effect, or one must accept that the associations observed are the result of the pleiotropic action of the mutation itself. In the present material the first appearance of the mutation is recent and can be dated. A study of its manifold effects might therefore provide further evidence on the relative importance of linkage and pleiotropy in determining character associations, and therefore assist in the planning of selection procedure.

2. THE MUTATION *ls* AND ITS PHENOTYPIC EXPRESSION

This mutation was first observed during 1951 growing among a crop of the pure line variety, Antimold B. The parent variety was bred at the John Innes and its history and parentage are known with

certainty. No trace of the mutation is to be found in the previous history of either the parents or grandparents of the variety, Antimold B. There can therefore be no question of selection having operated on the mutant genotype to establish character associations opposite to those present in the parent from which it arose.

The phenotypic effects of the mutation in the homozygous recessive phase comprise (*a*) suppression of branches in the axils of the leaves, (*b*) in certain genotypes suppression of apical growth at various stages of development, (*c*) suppression of corolla development: in this, its action resembles the known gene *ap* (apetalous), (*d*) deformed anthers which fail to remain united as a column around the style: this results in failure of pollination and in sterility, (*e*) reduction in flower number per inflorescence and (*f*) in certain gene backgrounds it forms partially apocarpous, parthenocarpic fruit which resemble the phenotype of the gene *gq* (grotesque). It seems clear that all these effects with the possible exception of (*d*) can be logically explained on the assumption that the locus controls the development of the primary meristem. All the expressions of the mutation show quantitative variation, and these can be intensified or reduced in segregating generations according to the genotypes of the parents. It may be noted that one of the effects associated with this mutant, namely flower number per inflorescence, is typical of characters that are used in experiments on the study of quantitative inheritance, and a detailed analysis of its genetic basis seemed therefore to be worthwhile.

3. VARIATION IN THE EFFECTS OF *ls ls* IN RELATION TO GENE BACKGROUND

(1) *Suppression of axillary branches*

Five F_2 progenies arising out of crossing *ls ls* with different pure line varieties were studied. The number of axillary branches (laterals) in the *ls ls* class of families H 56, 59 and 61 are given in fig. 1. H 59 and H 61 are derivatives of crossing *L. racemigerum* and *L. pimpinellifolium* respectively with *ls ls*, while H 56 is an intra-specific cross within *L. esculentum*. The two other intra-specific crosses resembled H 56 in lateral branch production and are therefore not given here. The plants were scored when fifteen fully developed leaves were present and the maximum number of laterals that could be recorded is therefore seventeen. It will be observed that the hybrids H 56 and H 59 behaved uniformly and very little variation in numbers of axillary branches was evident. The great majority of *ls ls* plants in these families were completely devoid of axillary branches and the maximum number of four branches recorded had a frequency of less than 0·2 per cent. By contrast, the majority of *ls ls* progeny derived from the *L. pimpinellifolium* cross had one developed lateral and the maximum number recorded in the cross was eleven. The three *esculentum* parents had been chosen because of their diversity of origin and type, but clearly

with respect to the modification of the suppressive action of *ls* on axillary meristems, the series contained little or no genetic diversity. In contrast to this, the inter-specific combination involving *pimpinellifolium* produced a wide and continuous range of modification, extending almost to normal phenotypic expression in the presence of *ls ls*.

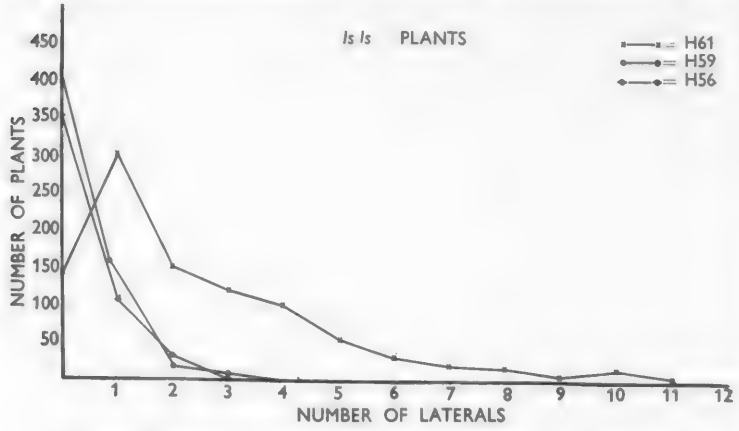

FIG. 1. Number of laterals on *ls ls* plants segregating in three F_2 families.

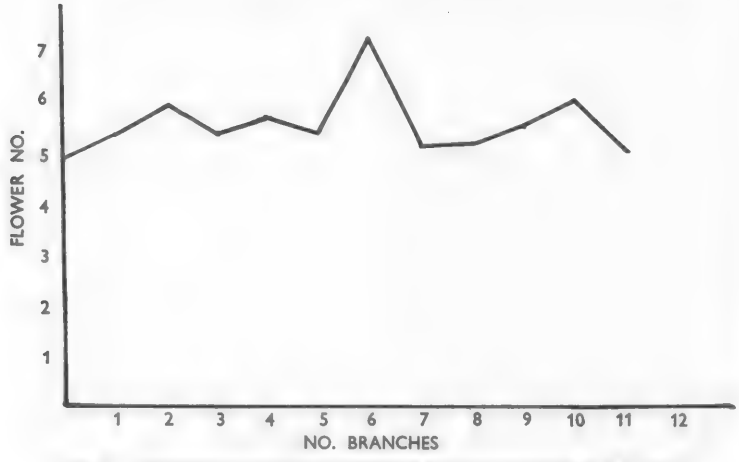

FIG. 2. Independence of number of branches and flower number in *ls ls* plants segregating in F_2.

None of the other expressions associated with the *ls* gene showed a correlated response with increased production of lateral branches, and it appears that the modifier effect of the gene background can discriminate between the several modifications. The independence of the two effects, branch number and flower number, can be seen in fig. 2.

(II) *Suppression of apical growth*

The control of terminal growth in *ls ls* phenotypes derived from the five different F_1 hybrids can be assessed from table 1. All the "+" phenotypes among the F_2 progenies had normal indeterminate growth. Recombinants from intra-specific crosses showed considerable variability of control in respect of this character. In the cross involving

TABLE 1

Percentage of ls ls *plants segregating in F_2 showing cessation of apical growth at different stages of development*

Parents of F_1 and family no.	Apical growth terminated after		Normal apical growth	Total
	1st inflorescence	2-7 inflorescences		
ls ls × Wonder of Italy (H 56)	6·06	35·49	58·44	231
ls ls × Earliana (H 57) . .	28·73	28·73	42·53	268
ls ls × Market King (H 55) .	16·77	83·23	□	477
ls ls × *L. racemigerum* (H 59) .	2·61	27·16	70·22	497
ls ls × *L. pimpinellifolium* (H 61)	0·20	2·30	97·48	477

the parent "Market King", apical growth was terminated at some stage of development in all plants of the *ls ls* class, whereas 58 per cent. of the comparable plants from "Wonder of Italy" continued growth normally. As with control of the development of lateral branches, the most successful source of genetic diversity for normalising

TABLE 2

Average number of flowers on first inflorescence in ls ls *phenotypes classified according to stage of cessation of apical growth*

Family no.	Apical growth terminated after		Normal apical growth	Total
	1st inflorescence	2-7 inflorescences		
H 55	5·68	6·58	□	477
H 56	3·71	3·78 *	7·88	231
H 57	4·81	6·86	7·88	268
H 59	3·15	4·01	4·86	497
H 61	5·00	4·00	5·46	477

* A large number of plants in family H 56 stopped growing after the second inflorescence, and thus the class resembles that in column 2 of this table.

apical growth was *L. pimpinellifolium*. *L. racemigerum* (H 59) while more effective than the *esculentum* parents was not as rich a source of modifiers as *L. pimpinellifolium*.

An analysis of flower number in the various growth classes among the *ls ls* genotypes showed that a severe reduction in flower number accompanied early cessation of apical development. The figures set out in table 2 indicate that the mean flower number in *ls ls* plants

showing cessation of apical development after the formation of the first inflorescence, is consistently lower than in *ls ls* plants in which apical growth was normal throughout the period of observation. Plants in which the apex failed after 2-7 inflorescences had developed, had intermediate flower numbers. None of the other effects normally expressed by *ls ls* genotypes showed detectable modifications which could be correlated with the stage at which apical development failed.

(iii) *Control of flower number*

The effect of the *ls* gene on flower number in several different gene backgrounds can be seen in table 3. The average number of

TABLE 3

Degree of expression of the manifold effects of ls *in* F_2 *and backcross families*

Parents * and family no.	No. of flowers on 1st inflorescence		No. of axillary branches	No. of petals per flower
	ls ls phenotypes	+ phenotypes	*ls ls* phenotypes	*ls ls* phenotypes
H 55 . . .	6·42±0·137	10·48	0·10	0·0
H 56 . . .	6·15±0·158	17·00	0·27	0·0
H 57 . . .	6·76±0·234	12·22	0·23	0·0
H 59 . . .	4·58±0·112	13·32	0·20	0·04
H 61 † . . .	5·42±0·160	15·14	2·59	0·85
H 69 (*ls ls*×P)†§ .	6·24±0·103	13·14	1·51	0·45
H 60 (P ‡×*ls ls*) .	6·22±0·171	13·38	1·11	0·41
[H 68 (*ls ls*×P ‡)] .	6·53±0·152	14·13	1·31	0·67
[(*ls ls*×P)×P] .	6·87±0·148	14·74	1·96	2·84
[(*ls ls*×P)×E §] .	6·59±0·179	10·86	1·72	1·15
[(*ls ls*×P)×P]×P .	6·42±0·112	17·44	1·21	3·34
[(*ls ls*×P)×P]×E .	5·98±0·104	9·76	1·37	1·70

* The parents of H 55-H 61 are as in table 1.
† Red fruited form of *pimpinellifolium*.
‡ Yellow fruited form of *pimpinellifolium*.
§ In the table P = *Lycopersicum pimpinellifolium* and E = *L. esculentum*.

axillary branches and average petal number per plant are also presented. The reduction in flower number was very marked in each family and the figures obtained for the *ls* class were on average over 50 per cent. less than in normal plants segregating in the same family. The range of the variation in the mutant and wild-type classes can be assessed from fig. 3. Apart from the progenies derived from *L. racemigerum* where the reduction was most severe, the means for flower number in table 3 are homogeneous. No correlation exists between the means for flower number, number of laterals and petal number in the *ls ls* class within the different families listed in table 3. Although the mean flower number in *ls ls* plants was similar in all families the mean petal number in progenies derived from *L. pimpinellifolium* was

significantly higher than in the other crosses. Thus the modifiers which affect petal number also behave differentially with respect to the manifold effects of the major gene mutation.

The backcross data given in table 3 indicate clearly that intensification of the *pimpinellifolium* background brings about a rapid advance towards normality of the corolla. In the backcrosses, maximum expression of corolla formation alone was selected, hence the other

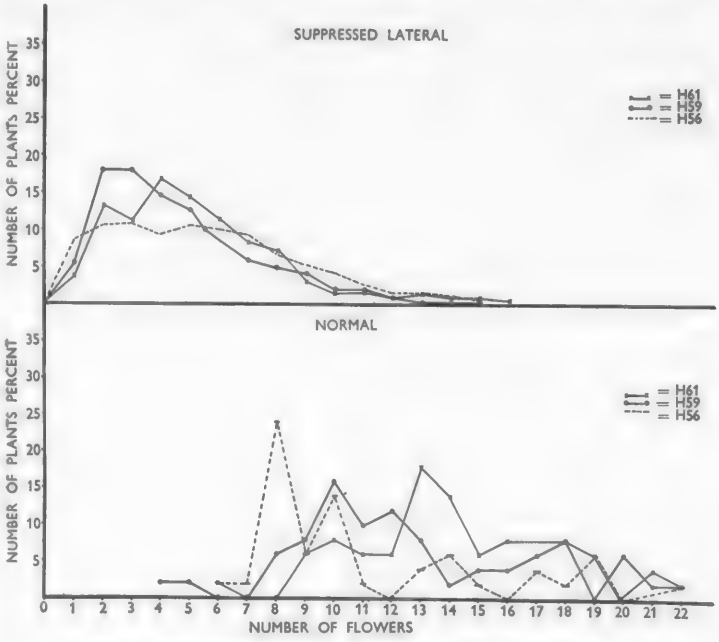

FIG. 3. Frequency distribution of flower number in *ls ls* and normal segregates in F_2 families.

phenotypic expressions remained virtually unchanged by backcrossing. The progressive advance under backcrossing shown here is consistent with the effects of a background of modifiers, and the extent of the variability released in the inter-specific, as opposed to intra-specific crosses, indicates that genetic elements of a kind that characterise large specific differences are involved.

Furthermore, although modification of each of the various effects of the mutant occurred in one or other of the families, the variation was continuous and no phenotype resembling a cross-over where one or more of the expressions had been restored to normal was observed. In all, segregating progenies amounting to over 57,000 individuals were recorded and the observations are summarised below. The class,

" Cross-over 1 ", refers to recombination between absence of laterals and one of the other phenotypic expressions, and the class, " Cross-over 2 " is the reciprocal recombinant.

Wild-type	" Cross-over 1 "	" Cross-over 2 "	*ls ls*	Total
43,994	0	0	13,274	57,268

The failure to recover cross-over types between absence of laterals and petal development in these large segregating populations is particularly significant, since there is no possibility that a full recombinant involving these two expressions would have remained undetected. The absence of cross-over phenotypes must also be considered in relation to the observations regarding the differential effects of the modifiers on the separate expressions of the mutant. If cross-over types had been detected, such differential effects of the modifiers could be explained on the basis of specific interactions with linked blocks of polygenes. Although the numbers observed cannot be considered adequate to preclude all possibility of very close linkage (Pontecorvo, 1959), the absence of a single recombinant between the component parts of the syndrome make this interpretation less probable, particularly since all the other evidence tends to emphasise the influence of the gene milieu on the various effects of the *ls* mutation.

4. INTERACTIONS BETWEEN *ls* AND OTHER CHROMOSOME REGIONS

The effect of the *ls* region on flower number provided a sensitive test for studying interactions between it and other marked regions of the chromosome complement. In all, thirteen marked regions, spread over seven different chromosomes, were studied. Unfortunately it was not possible at the time to study interactions with whole chromosomes adequately marked by suitable genes. Three marker stocks were crossed with homozygous *ls ls* parents carrying homozygous wild-type alleles at the marked loci. The single and double recessive classes involving the markers were recovered in F_2, and the flower number of each class scored. The results are set out in tables 4 and 5. The genetic constitution of the marker stocks can be gathered from the tables.

The effect of the *ls* gene on flower number (table 4) is not so marked in these families as in those described previously, and in family 71 although the *ls ls* genotype possessed the lowest average number of flowers, the difference between it and the wild-type is not significant. With the exception of the region marked by the gene *f* whose known effect is to increase floral parts (compartments of the ovary, stamens and corolla), no significant direct effect on flower number can be ascribed to any of the regions when present singly. When the marked regions are combined with *ls* (table 5) their effect on flower number in some cases becomes very striking. The combination *ls e* in family 72, *ls a* in families 70 and 72, and *ls dm* in family 71 clearly alter the

flower number as compared with *ls* +. It is almost certain, in spite of the lack of significance in family 71 as a whole, that the effect of *ls dm* in this progeny is real. Several other combinations, *ls y* in

TABLE 4

Flower numbers of F_2 plants homozygous for marker genes

Family 72			Family 71			Family 70		
Genotype	No.	Flower no.	Genotype	No.	Flower no.	Genotype	No.	Flower no.
e e	20	8·5	*dm dm*	21	8·1	*c c*	23	7·6
a a	20	8·6	*wt wt*	20	9·2	*a a*	20	7·1
t t	20	8·5	*f f*	20	13·5	*d d*	21	6·9
wf wf	20	9·1	*al al*	20	8·3	*l l*	20	8·1
y y	20	8·5	*ls ls*	43	6·8	*ls ls*	24	6·0
u u	12	8·4	+ +	20	7·2	+ +	73	7·4
ls ls	20	5·8						
+ +	20	9·2						
5 per cent. L.S.D. = 1·69			5 per cent. L.S.D. = 2·20			5 per cent. L.S.D. = 1·16		

family 72, *ls d* and *ls l* in family 70, and *ls wt* in family 71 would probably show significant effects on more extensive testing.

The behaviour of *ls a* is noteworthy since in family 70 it behaves in a negative direction, while in family 72 it increases flower number above the level of *ls* +. The variable interactions of *a*, if they are to be

TABLE 5

Flower numbers of F_2 plants homozygous for combinations of marker genes and ls

Family H 70			Family H 72			Family H 71		
Genotype	No.	Flower no.	Genotype	No.	Flower no.	Genotype	No.	Flower no.
+ +	40	7·35	+ +	20	9·15	+ +	20	7·20
ls +	73	6·02	*ls* +	20	5·85	*ls* +	43	6·77
ls c	24	5·71	*ls e*	18	4·11	*ls al*	14	6·90
ls a	37	5·14	*ls a*	18	7·88	*ls H*	19	6·10
ls d	28	5·39	*ls t*	14	5·78	*ls dm*	29	4·33
ls l	35	5·40	*ls y*	12	7·20	*ls wt*	10	7·55
			ls u	12	5·91	*ls f*	14	7·10
5 per cent. L.S.D. = 0·92			5 per cent. L.S.D. = 1·52			Not sign.		

explained on the basis of linkage, demand that the action of the linked units is reversible and that they function only in the presence of *ls*. Similarly, *dm* and *e* proved entirely neutral when present alone; their negative effect became evident only in combination with *ls*, while the combination *ls f* completely neutralised the positive effect due to *f* seen in table 4.

5. DISCUSSION

The point was made earlier that no conscious selection could have operated on this mutation since its first appearance in 1951. The variety Antimold B in which the mutant arose, as well as the parents of that variety, are all cultivated varieties in which high flower number is an expression of prime importance. Antimold B has an average flower number of 16·7 per inflorescence which is above average for forms of *esculentum*. The direction of selection in all the parental lines has therefore consistently been for high flower number, and one would expect an accumulation of positive genetic units controlling this expression to have occurred. The fact that on first appearance, the mutant gene affected flower number in a negative direction seems to rule out the possibility that quantitative factors accumulated under selection are operating. There is no evidence from meiosis or pollen viability that the mutation is a sizable deletion or inversion which could account for a large region comprising segments with separate functions being affected.

Several associations of the kind described here have been reported in the tomato (Currence, 1938; and Fogle and Currence, 1950). They have without exception been interpreted on the basis of close linkage between specific units having separate effects on the associated characters. On analysing these associations critically one finds that in every instance the quantitative character is shifted in the same direction irrespective of the marker gene or chromosome involved, and the direction is generally opposite to the direction of selection pressures acting on the wild-type. Currence (1938) reported on the four recessive markers *d p o* and *s*, and showed that the homozygous recessive genotypes of three of these was associated with lateness. These four genes are located on the same chromosome but the distance between *d* and *s* is 42 units indicating that along practically the whole length of the marked chromosome, only blocks of genes with negative effect can be detected. Again Fogle and Currence (1950) studied a further six markers distributed in four linkage groups, and with one reliable exception, the results followed those for *d p* and *s* as regards the unidirectional nature of the associations. These results are all the more significant since the direction of the expression in the continuous character remained constant in segregating recessives irrespective of the direction of expression of the character in the genotype from which the class was originally derived. For example, the markers *d* and *y* were found to be associated with lateness in segregating progenies of the two types of crosses, early *dd* × late *yy* and late *dd* × early *yy*. It is difficult to see how these results can be reconciled with the interpretation of linkage given by the authors.

One of the constant features of the modifier pattern found in the present material was that, in a given segregate, only one of the multiple expressions associated with the *ls* locus was affected. Apart from apical

growth and flower number, no correlated modifications appeared in *ls ls* plants even though some possessed an almost normal phenotype in respect of one of the quantitative effects. One interpretation of this effect would be to assume that the gene background interacts differentially with specific units of a linked system of quantitative genes. The remainder of the evidence, however, is firmly set against this explanation, and the basis of the unilateral behaviour of the gene background is probably due to interactions involving the direct and indirect effects of a single, basic error at the *ls* locus. That character modifications can occur singly in a multiple system based on one inheritance unit is clearly of the utmost importance in ensuring the survival of the advantageous components of a complex character.

It is highly significant that the most spectacular modifier influence was evident in F_2 progenies from inter-specific crosses: the release of variability from crosses within *L. esculentum* being in most cases quite negligible. If the modifications observed were the result of small quantitative effects at other loci, one might have expected intra-specific crosses to have been equally successful since, presumably, the stabilisation of characters like corolla development, apical growth and fertility must be considered advantageous to all species. The fact that only *L. pimpinellifolium* possessed the genetic constitution necessary for increasing the variation patterns of the several effects of the *ls* locus, suggests that the modifications are the result of inter-action between elements of the gene system which have attained a greater measure of diversification than is characteristic of intra-specific differences.

The studies on quantitative variation in *Prunus avium* and *Prunus persica* (Williams and Brown, 1956*a* and *b*) support the general conclusions reached here and underline what is already known concerning the positive role of major gene loci in controlling continuous variation. In most examples of this kind the limits of function of the major genes are not known and therefore the connection between the known action of the locus and the quantitative characters is not as obvious as in the case of the *ls* mutation, where most of the manifold effects, including flower number, can logically be related to the control of meristematic activity. Since the relation between gene and quantitative function is in general so complex, the part played by pleiotropy in determining character associations cannot be lightly dismissed when designing selection procedures.

6. SUMMARY

1. The manifold effects of the *ls* gene in the tomato, and the influence of diversity of genetic background on the various manifestations of the gene are described.

2. It is shown that effects of modifiers on one expression is not accompanied by a correlated response in the other. Thus the gene milieu can discriminate between the components of a complex series

of reactions resulting from one gene mutation and bring about modification of the manifold effects one at a time. This results in flexibility under selection, and enables the fixation of only those parts of the variability complex which have survival value.

3. No cross-over phenotype was detected in segregating progenies amounting to 57,268 plants.

4. The effects of interactions between *ls* and other marker genes on flower number, a typically metric trait, are described. It is suggested that the results are compatible only with an interpretation based on some form of pleiotropic action of the major gene mutation which responds to the influence of certain gene backgrounds.

5. The unidirectional nature of quantitative characters when associated with major gene mutations is discussed and is given as evidence supporting the hypothesis that indirect, direct or " spurious " pleiotropic action of major genes, can account for much of the quantitative variation that has hitherto been ascribed to linkage.

6. It is concluded that, where the aim is to resolve highly associated characters, wide-crossing can be expected in many instances to provide a better opportunity for selection than procedures designed to break linkages.

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COUSIN MARRIAGE AND THE EVOLUTION OF THE BREEDING SYSTEM IN MAN

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1. ANALYTICAL AND INTEGRAL GENETICS

The success of the Mendelian method in experimental breeding made it, sixty years ago, the natural model for understanding human heredity. The success of the model in interpreting the clinical entities which dominate medical training and in classifying them as Mendelian characters in due course reinforced this initial advantage. Lately, however, certain limitations of the method and the model have become evident. Man exists in natural outbreeding populations. His variation in these populations can only partly be reduced to terms of single gene differences. Faced with this discovery some students have inferred that such human variation cannot be genetically analysed or indeed analysed at all. Since, however, the strict Mendelian situation can hardly be expected to exist in outbreeding populations, this conclusion is unjustified.

To put the matter in another way: the genotype is, we may still agree, the sum of the genes. But a difference between genotypes is not just the sum of the differences between their genes. Indeed no one imagines that the genotype can be taken apart into polygenes, major genes, super-genes, with position effects, structural arrangements and so on. There is, therefore, one sense in which analysis in terms of genes or ultimately nucleotides is a suitable goal. But there is another sense in which it fails to tell us what we want to know, a sense in which an integral treatment is suitable and necessary.

This contrast was forced on me by the study of whole segments, whole chromosomes and whole nuclei in cells, in natural populations, and in hybrids, as I have described elsewhere (1956, 1957, 1958). Mather (1955) has seen the same problem in terms of quantitative variation and the breeding system, and especially by the exposure of the correlated response to selection. Dobzhansky and his colleagues have discovered it from the experimental treatment and chromosome study of natural populations, where they have recognised both the co-adaptation of segments and the integration of the genotype (Dobzhansky, 1950; Vetukhiv, 1954; Wallace, 1957*a*, *b*). These different kinds of approach lead to different statements of contrast and conflict. Each no doubt has its own physiological scope and validity.

The difference between these analytical and integral extremes, the difference between the single gene of Mendelian analysis and the whole genotype considered by Galton and Johannsen is almost of the order of

the difference between chemistry and biology. Both, like chemistry and biology, have their validity. But we cannot use one where the other is needed. Yet where man is concerned this is just what we see continually attempted. Analytical principles involving frequencies of analytical units, whether "genes" or "mutations", are directly applied to the non-analysable situation, for example the situation of radiation damage.

Now, in human heredity and variation certain properties most need integral treatment and suffer most from analytical treatment. These happen to be the properties of greatest importance for our survival and our evolution. They are the properties of temperament, of intelligence, of instinct, of their combination in behaviour, of viability and fertility, of resistance or susceptibility to infectious disease. These are integral properties. They depend on interactions of a great assembly of independently varying units. These interactions are on a scale which is not beyond conception, but it is beyond formal description or practical analysis.

TABLE 1

Relation between fertility of mother and daughter in the British Peerage (after Fisher, 1930, data of Pearson and Lee, 1899)

No. of children born to mother	1	5	11	>11
Average to daughter	3·0	4·0	5·1	6·4

This genetical principle is an expression of physiological and developmental situations. Take the basic evolutionary property of leaving descendants, a property which I am going to call fertility. This property depends on a sequence of elements: a desire for sexual intercourse, an ability to beget and bear offspring, a viability of embryos and offspring.* To these elements the development of birth control requires us to add one more, the desire to have offspring. These several elements overlap. The distinction between survival to birth and survival after birth is partly arbitrary. So is the distinction between not marrying and marrying but not having children after marriage. Thus we are bound to profit from considering the total reproductive result. Though the parts are arbitrary the whole is a reality: it is the great reality in life. In this we have the example of Galton before us. We also have Galton's and Pearson's methods of correlation in numbers of progeny between parents and offspring (table 1).

The observations of Galton and Pearson could be repeated with profit under the changed reproductive conditions of the present day. It would also be of great value to confirm the remarkable change in sex ratio shown by Galton's data (1869). Meanwhile we may note that these correlations must depend on two components whose relative value we can only surmise, namely heritability which has to be a

* This is the element which has been separately examined by most investigators who have found a depressing effect of inbreeding, *e.g.* Bemiss, 1858; Darwin, 1875; Stevenson, 1956; Morton *et al.*, 1956; Schull, 1958; Slatis, 1958.

primary agent, and assortative mating which will be a secondary agent. We know, following Pearson and Lee (1903), that assortative mating occurs in respect of every character in which the mates can be separately classified. Fertility is the one character in which they cannot be separated but it is one in which we have as much reason as in any other to expect assortative mating.

The method of attacking this problem of fertility that I wish to use, while omitting one of the two elements of the Mendelian experiment, the differential unit character, exploits the other, the change in the breeding system. The theory of this method has been discussed by Mather (1955) and the practice by myself (1955). Its technique in the human situation has a special character. Mendel's sequence: inbreeding, outbreeding, inbreeding, occurs in human populations only in special circumstances such as we find in Pitcairn Island and Tristan da Cunha. But we find the alternative, outbreeding, inbreeding, outbreeding in our own society if we follow the results of cousin marriage. For this we need to know two or three generations before the marriage and two or three generations after. We need to know something about the breeding system in the whole group. Is this possible?

2. EUROPEAN BREEDING SYSTEMS

The integral study of viability, fertility or intelligence by change of the breeding system requires that we shall know what the system is that is being changed. The human breeding system in class-differentiated human societies may be roughly defined in terms of two limits: (i) the limits to outbreeding and (ii) the limits to inbreeding.

(i) The limits to outbreeding are set by space, work, language or dialect, religion and economic or social status. All these are the environmental components in a reaction favouring kinship, or relationship of descent, among mates. The genetic component of this reaction may be described as the tendency to assortative mating. The two components reinforce the tendency to inbreed. For the phenotypic likeness of mates as expressed in assortative mating, and their relationship of descent, are two means of measuring inbreeding. To be sure they are both uncertain and for quite different reasons. Similar appearance may be due to similar genetic structure or not. Relationship of descent also may imply similarity of genetic structure or not. Nevertheless assortative mating and kinship will reinforce rather than counteract one another.

The environmental components themselves interact in complex ways. Thus social status divides the whole population into social classes. Space is a stronger barrier at the lower social levels. So also is religion. The earlier Christian community of Northern Europe was split by the Reformation into numerous non-interbreeding sects but at the Royal level these divisions are only partly effective: Protestant females may marry Catholic males. Only one of the Protestant

sects exist as a small minority at higher social and intellectual levels, that is the Quakers. The Jewish community at its Western edge is a larger breeding group but it exists at all social levels which divides it further. Other very small breeding groups have arisen from economic and political grounds, the merchant princes of Chios, Venice and Amsterdam, and elsewhere. By contrast with these the prosperous middle class in Britain following the industrial revolution must have been extremely outbred. Even here foci of inbreeding have quickly arisen, for example in connection with universities.

(ii) With regard to the limits to inbreeding all human societies make rules.* In Europe these limits are easily defined. The Catholic Church early set its face against inbreeding as permitted by Roman custom or Jewish law. This policy arose we may say from a habit of making rules for conduct. The reasons given by Gregory the Great in his letter to Augustine (*cit.* Bede) that cousin marriages give no offspring are scarcely to be taken seriously. Some of the rules have always been flagrantly and repeatedly broken by dispensation. Thus first-cousin marriages have been widespread in Catholic communities up to the present day. They are most frequent in the narrowing Royal caste where also uncle-niece marriages continued up to 1850.

The Reformation affected the inbreeding as well as the outbreeding limits. The Protestant churches, except the Swedish (Alström, 1958), gave up the nominal ban on cousin marriages but began to enforce a ban on uncle-niece marriages. Amongst Jewish minorities the pressure in favour of close inbreeding led to the highest frequency of uncle-niece marriage.

On account of these variations different communities in Europe provide us with all the contrasts we need: 16 per cent. of first-cousin and 3 per cent. of second-cousin marriages among Jews in Hohenzollern villages, the reverse among Catholics in a Swiss village (Neel *et al.*, 1949; Kilpatrick *et al.*, 1955). Even so, as we shall see, such statistics of cousin marriage give us very little idea of the real contrast. This arises from the consideration of still more specialised groups, very small sects such as the Mennonites and very small castes such as the Royal Families. With these we can discover the selective and evolutionary principles at work.

3. METHODS OF ENQUIRY

My object was to find out the genetic component in differences in the total reproductive potential or " fertility " in human marriages. I enquired first in the *Oxford Magazine* (December, 1957) for grandchildren of cousin marriages who would give me the total numbers of descendants of such marriages up to the great-grandchildren. From this beginning I was able to elaborate the question in the

* Following Darwin's lead in the *Descent of Man*, the documentary evidence of the restrictions on inbreeding in civilised man was compiled by Huth (1875). Here are to be found pedigrees of the Ptolemies, Herods, Antonines, and European Royal Families, as well as an account of the vagaries of Roman and Christian doctrine on the matter. Many of the properties of the Royal caste have recently been summarised by Moncrieffe and Pottinger (1956). Compare also : *Life and Letters of Charles Darwin*, 3, 129.

London *Observer* (January 1958) and in Messrs Sandoz's house journal *Triangle* (November 1958) which is addressed to the medical profession generally in the British Commonwealth and Western Europe.

The results of these enquiries were replies giving data of five kinds in increasing order of complexity :

(i) for single cousin marriages ancestral to the correspondent,
(ii) for others which were collateral or even unrelated to the correspondent,
(iii) for successive or grouped cousin marriages (including Royal marriages) often from experienced genealogists,
(iv) for " parallel sib marriages " with cousins and non-cousins,
(v) for " double test marriages " of one spouse with a cousin (or uncle) and a non-cousin.

The first class was the most important. Since it excluded marriages without grandchildren, it biased the sample in favour of fertility. But as H. G. Darwin pointed out, the numbers of marriageable cousins increase with the size of the family and exponentially with the generations. Cousin marriages are therefore inherently biased at their origin, or self-biased, in favour of high fertility. The third, fourth and fifth classes can be used in different ways to correct this situation.

The method I have developed was indicated in an earlier note (1955). It is to find out the following particulars (*Abbreviations* in Appendix):

(i) Dates of birth, marriage and death of the original cousins.
(ii) Total children, grandchildren or great-grandchildren born alive (c, gc, ggc in tables). Stillbirths were omitted since early data would be unreliable in this respect.
(iii) Total c and gc surviving to maturity (s) or between 22 and 24 years of age.
(iv) Total c and gc marrying (m).
(v) Total c and gc marrying and with issue (wi).

These last three I speak of as the successive " tests " in the reproductive cycle.

Later and especially in the double test marriages I enquired into the occurrence of previous cousin marriages and the type of breeding group of the original cousins. Thus at least seven generations had to be considered, and along some lines in some families as many as fourteen generations have been followed.

As I had expected, but with greater detail than I had expected, a wide range of breeding systems was revealed by my correspondents. They fell into three general groups :

(i) An extreme group which were known on social, political or religious grounds, or from their own pedigrees, to have been inbred for many generations.
(ii) An intermediate group in which cousin marriage (whether in a first or more remote degree) was known among the parents or grandparents of the critical marriage spouses.
(iii) Those with no evidence of inbreeding of either of these kinds.

Clearly this division is an arbitrary and provisional one. It conceals a continuous range of variation : it emphasises, however, a genuine bimodality in the breeding system. The large outbred group must include some slightly inbred stocks. But this will merely blunt the contrast I am trying to make.

This method turns out to be even more closely than might have been expected a mirror image of the Mendelian experiment. The following table shows their relations :

Generations	Mendel's experiment	Cousin marriage method
n	inbreed	outbreed
one	outbreed (P)	inbreed (cm)
n	inbreed (F_1, F_2, etc.)	outbreed (c, gc, ggc)

In addition, however, we can check the cousin marriage method by controls varying the degree and frequency of inbreeding in the prior generations.

It will be observed that no account is taken of the possibility of unknown illegitimacy of the parents or false paternity of the offspring who are wrongly included or wrongly excluded. But it will be seen that illegitimacy, or rather mistaken assignments of paternity, can only equalise the differences between classes of matings ; it cannot enhance them. Within classes it should of course enhance variances.

It will also be observed that certain events concerned in the lives of individuals can have no genetic component capable of selection in common with genuine genetic properties. Death in war and murder are two such types of event and I have therefore noted instances of these. All other relevant events I regard as apt to be genetically significant. Such are suicide, susceptibility to infectious disease, age of marriage, divorce, and others I shall refer to which are even more obviously genetic and selectable.

4. THE GENERAL POPULATION

The general results shown in table 2 give us a picture of the consequences of cousin marriage with progeny in the educated class in Britain where family records have been maintained during the last two centuries. They cover the range from one to fifteen children of the first marriage. They attempt the division into inbred and outbred stocks. They exclude only marriages without offspring and certain complex families which I shall consider later in detail (tables 3, 6, 7).

The summaries of the two groups of data provide us with a number of controlled comparisons from which we may draw tentative conclusions as follows:

(i) From the same average numbers of about six children per original marriage the inbred groups produce more than twice as many ggc as the outbred groups (28·6 against 12·8).

(ii) This difference is not due to a difference in the numbers of children per fertile marriage which show a similar decline in all groups from generation to generation following the national trend.

(iii) It is not due to any difference between the properties of the grandchildren of the two groups. Both of these have about 3 ggc p. m (wi) and about 50 per cent. of m (wi) p. gc. They thus act together as a control generation.

(iv) It is due to the survival, marriage and reproductive rates of the children being *depressed* to 40 per cent. in the outbred groups and *raised* to over 60 per cent. in the inbred groups, in comparison with the following control generation.

(v) The outbred group is large enough to divide into more and less fertile sections in respect of parents (9·1/4·0). We find that their fertility difference is maintained in the following c and gc generations.

(vi) Such a continuance over two generations results in the extreme disparity of 22·3/6·8 in ggc per original marriage. It implies an effect of assortative mating.

At this stage we are in a position to say something further about bias. It seems that the bias towards excessive fertility in the products of cousin marriages does not affect these inferences since the inbred and outbred groups which diverge in the first generation are equalised

TABLE 2

Descendants of marriages between first cousins

Data obtained from correspondents and historical records
Omitted are certain families in tables 5, 7, 8 and 14
Arranged in chronological order within the family number classes

TABLE 2A

Families without previous evidence of inbreeding

Name	Date	c				gc				ggc
		t	s	m	wi	t	s	m	wi	t
Ruskin	1818	1	1	1[1]	0	...	...	...	...	...
Hamilton	1897	1	1	1	1	1	1	1	1	4
Colbourne	1908	1	1	1	0	...	...	...	...	...
Ardenne	*c.* 1870	2	2	1	1	1	1	1	1	5
Sartoris (1)	1890	2	2	0	...	...	...	...	...	...
Sartoris (2)	1897	2	2	0	...	...	...	...	...	...
Davidson	1874	3	2	1	1	1	1	1	1	3
Dennis	1885	3	3	3	3	4	4	4	4	11+
Brown	*c.* 1810	4	3	3	2	19	12	10	9	30
Sutton	1848	4	4	3	2	3	2	1	0	...
Simon	1868	4	4	3	3	4	4	2	2	3
Ware	1892	4	3	3	2	3	3	2	2	5+
Hart	*c.* 1813	5	5	5	2	6	6	4	4	7
Candy[2]	*c.* 1825	5	3	2	1[3]	19	13	11	8	28
Bradish	1840	5	5	3	1	9	9	2	1	2
Wade	1858	5	5	4[4]	2	6	5	5	4	5
Braun	1860	5	2	2	2	6	6	4	3	5
Cooper	1872	5	4	4	4	6	5	5	5	9
King	1813	6	5	3	1	13	10	8	5	13
Freestone	*c.* 1820	6+[5]	6	3[6]	2	12	12	7	6	13
Sillar	1862	6	3	2	2	5	5	4	3	9
Hick	1882	6	5	2	2[7]	6	6	6	6	8+
Gwynn	1889	6	4	2	0	...	...	...	...	...
Berry	*c.* 1895	6[8]	3	3	1	2	2	2	2	4+
Boswell[9]	1769	7	5	2	2	9	6	5	4	14+[10]
Thornton-Duesbury	1865	7	7	2	1	2	2	0	...	...
Folwell	1890	7	2	2	2	3	2	2	2	5+
Macleod[11]	*c.* 1855	8	5	5	4	10	8[12]	5	5	11
Whone	*c.* 1900	8	4	4	4	12	12	8	4+	10+
Watson	*c.* 1815	9	6[13]	4	3	9	8	5	5	11+
M'Conaghy	1861	9	7	3	2	14	9	9	9	24
Abraham	*c.* 1855[14]	10	8	6	6	21[15]	14	13	11	15
Scott	*c.* 1856	11	11	4	4	10	5	4	4	15
Kindersley[16]	1857	11	10	7	5	13	12	9+	7	18
Callender[17]	1858	11	10	6	6	21	16	13	10	33
"Reid"	1853	12	9	4	3	10	8	7[18]	5	9
Pittmann	1826	13	10[19]	3	3	15	14	11	10	23
Trench[20]	1832	14	10	8	6	35	31	23	15	35+
Walker[21]	1867	15	13	11	10	32	30	26	21	54

[1] Marriage not consummated
[2] Rev. Charles Candy
[3] Rev. Herbert Candy
[4] One married three times without issue
[5] Possible infant deaths not recorded
[6] Three sibs married 3 unrelated sibs
[7] Another cm
[8] One killed in war
[9] James Boswell (1740-95)
[10] Not all traceable
[11] Died at 38
[12] One killed
[13] Two unmd. born blind
[14] Jewish : *m.* in Jamaica
[15] Three killed, 4 others died
[16] See table 13
[17] See table 15
[18] Two killed
[19] One emigrated, no record ; one suicide
[20] See table 4
[21] See table 5

in the second. Nor are the families concerned or the *propositi* aware of the genetic theory which distinguishes the two groups. The bias which I am inclined to suspect, not a severe one, favours bimodality or bipolarity. People are naturally interested in demonstrating the extremes which are most effectively demonstrable, whether these prove or disprove the hypothesis proposed to them.

TABLE 2A (*continued*)

Name	No.	c				gc				ggc
		t	s	m	wi	t	s	m	wi	t
TOTALS										
1-6 . . .	24 m	**97**	78	53	35	**126**	102	80	67	**164+**
cpm (wi) . .		*4·0*				*3·6*				*2·45*
cp original m .		*4·0*				*5·3* (× 1·3)				*6·8* (× 1·7)
Percentage passing successive tests		...	80	68	66	...	81	78	84	...
			36 per cent.				53 per cent.			
7-15 . . .	15 m	**137**	107	68	59	**216**	168	132	105	**335+**
cpm (wi) . .		*9·1*				*3·7*				*3·2*
cp original m .		*9·1*				*14·4* (× 1·6)				*22·3* (× 2·5)
Percentage passing successive tests		...	78	64	87	...	78	78	79	
			43 per cent.				48 per cent.			
GRAND TOTALS .	39 m	**234**	185	121	94	**342**	270	212	172	**499+**
cpm (wi) . .		*6·0*				*3·6*				*2·9*
cp original m .		*6·0*				*8·8* (× 1·5)				*12·8* (× 2·1)
Percentage passing successive tests		...	79	66	77*	...	79	78	81*	...
			40 per cent.				50 per cent.			

* The 1951 British Census records as having had live-born children 88 per cent. of all marriages that have lasted over 15 years (Campbell, 1958), *i.e.* 12 per cent. of sterility.

This interest in simple demonstration is responsible perhaps for the clear statement of causes of the depression in survival, marriage and fertility in the first generation in table 2A.

The causes of the depression effect that are given by correspondents for each of the three stages of the life-cycle that I have distinguished include the following:

1. *Survival:* pyloric stenosis, epilepsy, diabetes, cancer.
2. *Marriage:* blindness, intersexuality, insanity, lack of interest in the opposite sex, or in either sex.

3. *Reproduction:* (in women) acute dysmenorrhœa, toxæmia of pregnancy, miscarriage and difficult parturition (leading in one family to Cæsarean section in mother and daughter).

Defects such as blindness (*e.g.* in table 3) are no doubt often due to the segregation of major-gene recessives so well known in cousin marriages. The majority of defects, however, escape classification. One of these classes, which is increased in the progeny of table 2A,

TABLE 2B

Families from small-groups or with successive cm (omitting DTM)

Name	Date	c				gc				ggc
		I	s	III	wi	t	II	III	wi	t
Grubb [1]	1879	3	3	2	2	5	5	4	3	10
Spencer [2]	*c.* 1790	4	4	3	3	7	6	4?	4	17
Gilpin (6a)[3]	1855	4	3	2	2	10	7	5	5	17
Davies [4]	1835	5	4	1	1	14	9	5	5	22
T. F. Buxton [5]	1845	5	5	4	4	20	19	15	10	39
E. N. Buxton [6]	1835	7	6	6	6	38	36	28	20	62
" White " [7]	1870	7	6	6	6	17	17	14	12	35+
Butland [8]	1858	11	10	8	7	17	17	11	8	23
Shewell [9]	1874	11	9	5	5	18	18	15	12+	32+
Total	9 m	57	50	37	35	146	136	101	79+	257+
pm (wi)		6·3				4·2				3·3
p original m		6·3				16·2 (×2·6)				28·6 (×4·5)
Percentage passing successive tests		...	88	74	95	...	93	74	79+	...
			61 per cent.				54 per cent.			

[1] Irish Quaker family
[2] See table 6
[3] See table 10
[4] See table 14
[5] Quaker family
[6] Spouses gc of the 3rd D. of Marlborough
[7] Scm: two common gps were first cousins
[8] See table 10
[9] White Bermudian family

is that of those who reach mature years but do not marry: they prefer celibacy.*

They are due to the production of new and untested combinations. When such combinations are unfavourable we are accustomed to refer to them as examples of unbalance. But here precisely the same process gives rise to a small proportion of individuals—5 to 10 per cent. —scattered through the children of cousin marriage progenies in outbred stocks whose fertility is not depressed but enhanced.

* Galton (1869) considered, not unreasonably, that the celibacy of the mediæval clergy, so far as it was respected, prevented the proportionate breeding of a useful fraction of society to the disadvantage of succeeding generations. But between 10 and 20 per cent. of most populations never breed in any case although no vows of celibacy are imposed upon them. In so far as they fail to breed for genetic reasons it follows that the vow is secondary, the genotype is primary. They make a virtue of necessity, and only our instinctive belief in the power of free will has prevented our recognising the sequence of events.

The consequence of this recombination is that while the children in the inbred stocks are fairly uniform in behaviour, those in the outbred stocks show an extravagant range of variation. It is seen *within* large families and *between* small ones. On the one hand, in table 2B, there are the Grubb, Buxton, Shewell and Butland families, homogeneous and steadily expanding, some slowly, some rapidly. On the other hand, in table 2A there are the Brown, Candy and King families where most sibs do not marry or have no offspring while others have

TABLE 3

Descendants of THOMAS NOCK, *b. 1829, m. 1850, Sophia Johnson, half cousin*

c							gc				ggc
t	■	m	wi		born	m	t	s	m	wi	t
14 [1]	9	7	7	♂	1851	1871	10	5	5	5	13 [2]
				♀	1853	1869	12	■	2	2	■
				♀	1860	1882	8	5	5	5*	6
				♂	1864	1889	3	■	2	■	3
				♂	1865	1890	5	5	5	5	7
				♂	1865	1897	3	3	3	2	3 [3]
				♀	1869	1899	4 [4]	1	1	1	6
					Total	.	45	27	23	22	48

[1] Includes six born blind, unmarried; also one pair two-egg twins (bracketed, *b.* 1865). Excludes two pairs twins born dead.
[2] Includes two pairs of twins.
[3] Includes one pair of twins: one married a twin and had twins in 1957.
[4] Includes one born blind.

Notes: (i) High fertility and twinning combined with reproduction impaired by a visible defect arising from cm.
(ii) Drop in birth rate after 1890 coincides with drop in infant mortality.

* *Source*: Mr Walter Wilson of Ulverston.

up to nineteen children. Similarly in the Henderson pedigree (table 15B, 2*a*).

Our division, of course, is arbitrary. As we saw, there must be a continuous gradation between the extremes. We find the intermediate situation in the Trench family belonging to the Anglo-Irish landowning class which has no doubt been moderately inbred for 250 years (tables 2A and 4). We also find it in the Davies family which does not come from an inbred group but merely has one earlier cousin marriage (table 2B). And finally in the Walker family (tables 2A and 5) with no particular evidence of prior inbreeding we have a pedigree of the uniform type. These difficulties of classification, however, do not prevent me thinking that the modes are near the extremes and the intermediates are less abundant.

Now, in the inbred stocks which fail to show an inbreeding depression, it would seem that there is not enough heterogeneity present to

TABLE 4

Descendants of RICHARD CHENEVIX TRENCH *(1807-86), Archbishop of Dublin, m. 1832, first cousin, Hon. Frances Mary Trench (1809-90)*

		c				gc				ggc
Name	Date	t	s	m	wi	t	s	m	wi	t
Trench	1832	14 [1]	10	8	6	6 5 8 3 7 6	4 5 7 3 7 5	3 3 6 2 5 4	1 2 5 1 3 3	1 2+ 14 5 4+ 7
						35	31	23	15	35+

[1] 8 sons, 6 daughters.

Source: Mr C. E. F. Trench, Drogheda, Eire.

TABLE 5

Descendants of Dr THOMAS JAMES WALKER *of Peterborough (1835-1916), m. c. 1867, his first cousin, Mary Elizabeth Walker (1845-1915) daughter of the Vicar of Newmarket*

c				gc				ggc
t	s	m	wi	t	s	m	wi	t
15	13	11	10	5 2 3 5 1 7 2 2 3 2	5 2 3 5 1 7 [1] 2 2 3 1	4 1 3 5 1 5 1 1 2 2	3 1 1 4 1 5 1 1 1 2	8 1 1 6 3 10 2 4 2 5
				32	32	26	21	54

[1] One injured in spine in 1914 war, unmarried.

Source: Mrs Freda Gill, Chesterwood Grange, Hexham.

cause a high proportion of unfavourable combinations to appear on inbreeding. Or to put the matter in another way, the unfavourable combinations so far as they concern fertility have already been cleaned out of these stocks.

To test this view I have examined the different kinds of conditions under which inbreeding develops and its effects on fertility. We may roughly but conveniently distinguish three kinds of situation:

(i) Social or economic origin.
(ii) Religious origin.
(iii) Royal families where assortative mating and even natural selection to some extent lapse.

There is of course no limit to the number of such stable systems that could be studied in different parts of the world. It is, however, the systems that exist in Europe that are of the most interest, on account of their instability and also their documentation.

5. INBRED GROUPS

(i) *Social or economic inbreeding*

The development of cousin marriages may be readily followed from the prolific Gilpin and Wedgwood pedigrees. In the Gilpin family the first cousin marriage extracted, following heavy elimination, fertile strains, *i.e.* favourable recombinations. In these, after an interval of one generation, further cousin marriages occurred, one being between double first cousins. The Wedgwood family began, in this respect, with a third-cousin marriage which was followed, after an interval of two generations, by four cousin marriages, one again being between double first cousins. Here the third-cousin marriage does not seem to have mitigated the effects of the subsequent inbreeding, for the survival and fertility of the children was low. Only in one family, the descendants of Charles Darwin, has a highly fertile strain emerged from the recombination (tables 6 and 7).

The descendants of the Rev. Charles Candy (1800-1890) (table 2A) show similarly the pattern by which successive cousin marriages originate. He married his first cousin and the result was typical of cousin marriage in an outbred stock. They had four sons; three survived, two married, but only one had issue. This was Herbert Candy (1832-1893) who married twice, once a near relative, Margaret Spence (five children), and once an unrelated daughter of a cousin marriage, Mary Davies (fourteen children). Hence from this one surviving child were descended twenty-eight great-grandchildren.

Thus we have the emergence of highly fertile stocks capable of further inbreeding from only single individuals among the offspring of cousin marriage in outbred stocks. These we may call *founder-marriages*. They have their origins in special social, economic, and intellectual situations. Such marriages are seen establishing new lines in the Gilpin, Wedgwood and Candy, and also in the White and the Brown families. The proportions of these successes seem to be small. But they show us how the persistent inbred groups in Quakers, Jews and Royal families probably began.

TABLE 6

Successive cousin marriages

The GILPIN *family of Scaleby Castle, Cumberland, by generations*

1. William Gilpin (1657-1724) *m.* Mary Fletcher (*b.* 1654)
3. Rev. Wm. Gilpin (1724-1804) *m.* Margaret Gilpin (1725-1807)
4. Rev. Wm. Gilpin (1757-1848) *m.* Elizabeth Farish (1760-1831)
6*a*. Richard Brownlow Benson (*b.* 1831) *m.* Eliz. Barbara Gilpin (*b.* 1830)
6*b*. Charles Benson (1826-1911) *m.* Henrietta Emily Gilpin (1832-1880)

Generation	Date	c				gc				ggc
		t	s	m	wi	t	s	m	wi	t
1	1688	11	8	6	4	29	15	10	7 [1]	*c.* 39 [2]
3 [3]	1753	4	2	2	2	26 [4]	10	3	2	12
4	*c.* 1785	15	10	3	2	12	9	8	7 [5]	42
6*a*	1855	4	3	2	2	10	9	5	5	17
6*b*	*c.* 1856	7	6	3	2	12	12	8+	8+	18+

[1] Including both parents in 3. [2] Including both parents in 4.
[3] Double first cousins. [4] One of the two families is untraced after birth.
[5] Including both parents in both 6*a* and 6*b*, which were parallel: two brothers to two sisters.

Source: Mr George Benson, of Highgate West Hill.

TABLE 7

Successive cousin marriages of the WEDGWOOD *family, descended from* JOSIAH WEDGWOOD I *(1730-95) of Etruria, who married in 1760, Sarah Wedgwood (1734-1815) his third cousin*

Generation	Husband	Date	*c*				gc				ggc
			t	s	m	wi	t	s	m	wi	t
1	Josiah W. I . .	1730-95	8	6	3	3	22	20	13	11 [1]	64 [2]
3*a*	Charles Darwin .	1809-84	10	7	6	3	9	9	8	7	28
3*b*	Hensleigh W. . .	1803-91	6	6	4	3	5 [3]	4	3	2	7
3*c*	Henry Allen W. [4] .	1799-1885	5	5	4	2	1	1	4	1	2
3*d*	Josiah W. III . .	1795-1880	4	3	1	2	7	7 [5]	5	2	7
4	Godfrey W. [6] . .	1833-1905	1	1	1	0	...				
6	Josiah C. W. [7] . .	1872-1943	7	7	5	4	14	12	6+	...	18+
3*a-d*	Total . .	...	25	21	16	10	29	28	20	12	44

[1] Two gc married unrelated wives and had no issue.
[2] Doubling the 19 ggc who were descended in two lines owing to cm.
[3] One killed at 22.
[4] A double 1st cm: it produces fewer ggc than other cm except 4.
[5] Two of these 7 were killed (one at 34 unmd., one at 33 with 3 ch. *i.e.* fertility curtailed).
[6] Married a daughter of 3*b*, *i.e.* of a cm. This was a second marriage (see double test marriages).
[7] 1st Baron Wedgwood. [6,7] descended from no previous cms since Josiah W. I.

Source: Hon. Mrs Helen Pease of Cambridge.

(ii) *Religious minorities*

Jewish communities in Europe seem until recently to have been closely inbred. This was partly due to their position as a strict religious minority of great antiquity and partly to their discriminating social stratification. The distribution of cousin marriages in a particular group long residing in the region of Birmingham is shown in table 8.

TABLE 8

Distribution of 32 cousin marriages in the Joseph connection by degrees

1st	1·5	2nd	2·5	3rd	3·5	4th	4·5	5·5	6·5
10	1	7	1	1	3	3	4	1	1

It indicates a preference for close over less close inbreeding. The results (in table 9) are regular. They are so regular that we can see the fall in numbers of progeny from generation to generation strictly

TABLE 9

Ten marriages of first cousins in the Joseph connection

No.	Date	c			gc
		t (cpm)	m	wi	t (cpm)
1.	*c.* 1800	10	4	4	27
2.	*c.* 1810	4	3	2	4
3.	*c.* 1844	3	...	...	...
4.	*c.* 1855	3	1	1	1
5.	*c.* 1860	8	4	4	14
	Total	28 (5·6)	12	11	46 (4·2)
6.	*c.* 1876	4	2	2	5
7.	*c.* 1880	1	1	...	...
8.	*c.* 1895	3	3	3	6
9.	*c.* 1904	3	3	2	7
10.	*c.* 1906	2	1	...	...
	Total	13 (2·6)	10	7	18 (2·6)

Source: Mr Anthony Joseph, Trinity College, Cambridge.

in keeping with the national trend. And there is no depression produced by the cousin marriage.

The same result is shown by the Buxton family records (table 10). This family is derived from two closely inbred communities, the Quakers and the Independents. The two marriages shown are between

two pairs of siblings. Again they show high regularity, with a fall in numbers of gc in keeping with the national trend, and no fall in fertility between the parents and the children.

TABLE 10

Parallel first cousin marriages of sibs in an inbred community (incomplete data)

A. Edward North Buxton, 2nd Bart. (1813-1895) *m.* 1835 Catherine Gurney

c				gc				ggc
i	s	m	wi	t	s	iii	wi	t
8	[illegible]	[illegible]	[illegible]	10	10	9	[illegible]	29
				10	10	7	6	23
				7	[illegible]	5	4	14
				4	4	3	2	5
				2	2	1	1	4
				7	7	[illegible]	2	5
				[illegible]	3	3	3	6
				5	2+	2+	2+	4+
Total				48	45+	36+	28+	90+

B. Thomas Fowell Buxton (1821-1908) *m.* 1848 Rachel Jane Gurney

c				gc				ggc
t	s	m	wi	t	s	m	wi	t
11	11	9	8	7	7	5	5	25
				9	8	8	7	17+
				3	3	2	2	9+
				5	4	3	3	7+
				6	5	3	1	2+
				6	6	6	4+	4+
				7	7	5	5	9+
Total				41	40	32	27+	73+

(iii) *Mennonites or Hutterites*

This sect arose in Central Europe in 1528, and on account of its strict anabaptist principles it has been inbred for over 300 years: the products of outbreeding are excluded. The group early multiplied to about 15,000 but were nearly exterminated by later persecutions. Sixty fled to Russia in 1762, and of their descendants some returned to Central Europe in 1874 while—to avoid military service—about 300 migrated to South Dakota, whence their descendants have spread

TABLE 11

Mennonite pedigree. Shows all male descendants of Moses Göring in male line and all their female children. Probably includes none who died before maturity

Sex	C	gc (from 4 ♂ c)	ggc (from 7 ♂ gc)	gggc (from 29 ♂ ggc)
♂	4	4+0+1+4 9 (8 m, 7 wi)	7+6+1+4+3+5+3 29 (29 m, 29 wi)	2, 1, 2, 6, 1, 3, 3 : 5, 0, 4 6, 7, 8 : 2 : 2, 1, 2, 1 5, 6, 2 : 6, 1, 1, 5, 1 4, 1, 2 90 (not all m yet)
♀	5	[4+1+1+6] 12	[2+5+1+4+4+2+1] 19	4, 6, 1, 2, 2, 3, 4 : 1, 1, 3 5, 3, 4, : 1 : 1, 3, 3, 4 2, 3, 2 : 2, 6, 4, 2, 2 2, 2, 0 80
Total	9	8+1+2+10 21	9+11+2+8+7+7+4 48	6, 7, 3, 8, 3, 6, 7 : 6, 1, 3 11, 10, 12 : 3 : 3, 4, 5 5 : 7, 9, 4 : 8, 7, 5, 7 3 : 6, 3, 2 170 gggc
Estimated period of birth	1787-1810	1808-1850	1830-1890	1860-1950
Surviving c pm		$\frac{21}{4} = 5{\cdot}25$	$\frac{48}{8} = 6{\cdot}00$	$\frac{170}{29} = 5{\cdot}86$

Note. Moses Göring of Mömpelsgard (Montbéliard, France) (married *c.* 1785). Moved to Einsie (Austria), 1790, Michelsdorf (Poland), 1797, Edwardsdorf (Russia), 1815, Waldheim, 1837. Descenda to Kotusowka, 1863, Kansas and Dakota, 1874.

All ancestors had had regular 1st, 2nd, or 3rd cousin marriages (single or double) for several gener tions. This continued in the pedigree. Thus some would be descended in more than one line fr Moses Göring. Only one of these was *double* in the male line however (*i.e.* marriages between t Görings). Hence there is little repetition.

Source : Petronella Göring of Vienna IV, 50, Mostgasse 8a.

TABLE 11A

Progeny in third and fourth generations from Moses Göring showing positive correlation in fertility of successive generations (data in table 11)

Nos. of ggc in 7 families		Nos. of gggc from ♂	
♂+♀	♂	Total	Mean
2	1	11	2·0
4	3	11	3·7
7	3	13	4·3
7	5	30	6·0
8	4	17	4·3
9	7	40	5·7
11	6	49	8·2

widely and multiplied to about 9000 dispersed in about 100 village colonies. They have ceased to be a minority; they have become a self-sufficient society. These are now further divided into three separate inbred groups and bear only fourteen family names. Evidence of their reproductive capacity and its evolution comes from two sources.

My first source is the pedigree of the descendants in the male line of Moses Göring (table 11). It will be seen that their net fertility is high and slightly increasing: from 5·25 per marriage to about 6·00 over three generations. Not only this, but hardly any who survive fail to get married and hardly any, indeed latterly none, who marry fail to have issue, the number of issue varying from one to twelve. In this variation the gcs are correlated with their parents (table 11A).

My second source is the admirable account by Eaton and Mayer of the American community, many of whom are descended from Moses Göring. This shows again that the fertility, as recorded by the full birth rate in the 1950 census, is still increasing: from 9·2 to 10·9 per marriage over a period of thirty years. Hence the multiplication of the population nineteen-fold in the last eighty years.

A situation of this kind, high and increasing fertility, should arise if very high fertility (being genetically determined) is selectively advantageous. This is probably not the case in most human societies. The conditions of the Mennonite community in the United States do, however, explain such a selective advantage. These conditions are three-fold: (i) A community adapted by industry and intelligence to the agricultural work which uniformly maintains its progeny and for which opportunities are unlimited. (ii) Regular inbreeding ensuring genetic homogeneity within small groups; since "swarming" takes place when they reach a certain size, these groups maintain a membership of ten to twenty families. (iii) A communistic rule that in the last resort the group is responsible for the aged and the infants in each family. So long as the community prospers therefore and land is unrestricted, children cannot suffer from being too numerous.

We can now examine how these rules apply in other groups.

(iv) *Royal families*

The Royal families of Europe resemble the Mennonites in many respects. Like the Mennonites they have inbred and kept the breeding groups small by splitting into inbred sub-groups, the Protestant, the Catholic and the Orthodox. Like the Mennonites, they have outbred occasionally (by morganatic marriages). But they have excluded the products of outbreeding from the group, at least during the golden age with which we are dealing. Like the Mennonites they have not needed to trouble about providing for the offspring. The community will look after that. But, unlike the Mennonites, they are supported by a community which is not their own mating group. It is a whole nation. Selection in Royal families has therefore been much relaxed and the

TABLE 12

Progeny derived from 37 first cousin marriages between 1764 and 1886 among European Royal families

	C/P	Date of m	c				gc				ggc
			t	s	m	wi	t	s	m	wi	t
George IV, Gt. Britain	P	1795	1	1	1	0	0		...	...	...
Pedro, Spain	C	1810	1	1	1	1	4	4	4	3	7
Ernst-August, Hanover	P	1815	1	1	1	1	3	3	2	1	6
Günther, Schwarzburg-R	P	1816	1	0	0	0	0				...
Georg, Anhalt	P	1825	1	1	0	0	0				...
Gustav Wasa, Sweden	P	1830	1	1	1	0	0				...
Friedrich-W, Meck. Str.	P	1843	1	1	1	1	4	3	2	1	4
Friedrich, Württ.	P	1845	1	1	1	1	2	1	1	1	2
Karl Theodor, Bavaria	C	1864	1	1	1	1	8	8	6	5	18
Wilhelm Meck.-Schw.	P	1865	1	1	1	1	3	3	2	1	3
Umberto I, Italy	C	1868	1	1	1	1	5	5	5	5	17
Louis, Parma	C	1798	2	2	2	1	2	1	1	1	4
Henri d'Aumerle	C	1844	2	0	0	0	0				...
Friedrich, Nds.	P	1820	2	2	2	2	6	6	4	4	14
Antoine, Orléans	C	1886	2	2	2	1	3	2	1	1	4
Totals (15 families)			*19*	*16*	*15*	*11*	*40*	*36*	*28*	*23*	*79*
Wilhelm I (b^1) Hesse-C.	P	1764	3	3	3	2	5	5	4	3	12
Ferdinand III (b^2), Tuscany	C	1790	3+	3	2	2	9	9	7	7	34
Willem I, Nds.	P	1791	3	3	3	3	8	8	8	7	18
Wilhelm I, Württ.	P	1819	3	3	3	2	6	6	5	4	8
Günther, Schwarzburg-S.	P	1827	3	3	1	0	0				...
Willem III, Nds.	P	1839	3	2	0	0	0				...
Karl Alex., Saxe-W.	P	1842	3	3	3	2	6	5	5	4	11
Eugen, Württ.	P	1843	3	3	3	1	2	2	2	2	6
Paul-Friedrich, Meck.-Schw.	P	1881	3	2	1	0	0				...
Ludwig Ferd., Bavaria	C	1883	3	3	2	2	6	5	3	3	9
Totals (10 families)			*30+*	*28*	*21*	*14*	*42*	*40*	*34*	*30*	*88*
Karl (b^1) Hesse-C.	P	1766	4	4	3	2	11	11	8	2	11
Wilhelm, Prussia	P	1804	4	4	3	3	7	6	4	4	11
Franz-Josef I, Austria	C	1854	4	3	3	3	14	14	12	10	56
Ludwig II, Hesse-D.	P	1804	5	4	4	3	16	15	14	12	43
V.-Emmanuel II, Italy	C	1842	5	4	4	4	10	10	6	5	12
Isabella II, Spain	C	1846	5	4	4	3	8	8	7	6	22
Karl, Baden	P	1774	6	5	5	5	18	16	15	12	54
Ludwig, Hesse-D.	P	1777	6	5	3	3	8	5	4	3	16
Franz I (b^2), Austria	C	1791	6+	6	6	4	11+	11	8	7	26
Philippe, Orléans	C	1865	6	6	6	4	12	12	10	9	29
Totals (10 families)			*51+*	*45*	*41*	*34*	*115*	*88*	*70*	*70*	*268*
Victoria, Gt. Britain	P	1840	9	9	9	8	34	34	26	23	84
Alfonso, B.-Sicilies	C	1868	11	11	9	7	28	26	17	16	49

* Numbers of ggc of Isabella and Victoria each include 4 doubled owing to cm among gcs of original cm.

results as shown by our fertility records have been much less uniform than with the Mennonites. Selection is not directed; it is erratic. Fertility is very variable. On the average it is not high. And it does not increase from generation to generation (table 12).

Comparison of the Royal families with the general British population, inbred and outbred, shows the striking constancy of results of the Royal cousin marriages. There is no depression or elevation of the numbers of cpm (wi), which remain 3·4 or 3·5 or of the proportion of successes

SUMMARY OF TABLE 12

(Royal cm)

Nos. of C	Nos. of m	c				gc				ggc
Totals										
1-6 . . .	35	100+	89	77	59	197+	184	150	124	447
cpm(wi) . .		*2·9*				*3·3*				*3·6*
9, 11 . . .	8	20	20	18	15	62	60	43	39	133
cpm(wi) . .		*10·0*				*4·1*				*2·3*
Grand Total . .	37	120+	109	95	74	259+	244	193	163	580
cpm(wi) . .		*3·3*				*3·5*				*3·6*
cpm (original) .		*3·3*				*7·0*				*15·7*
Percentage passing successive tests	...	89	87		78	...	94	79	85	
		61 per cent.					63 per cent.			

Notes on Table 12

(i) Classified into two main groups, Catholic (14) and Protestant (23).
(ii) Arranged by numbers of children of original marriage.
(iii) Some of the parents are themselves offspring of cousin or uncle-niece marriages.
(iv) Two pairs of brothers show close similarity in numbers of descendants. b^1 married non-sisters; b^2 married sisters.

Source: Mr R. S. Lucas of the University of Nottingham.

in survival, marriage or reproduction between the first and second generation, which remains 61 per cent. or 63 per cent. There is no reason why there should be any change, because all marriages are between cousins of some degree within a homogeneous group, and the distinction between first and second generations therefore lapses.

Royal marriages in the period we are considering were usually political marriages. They should not, therefore, show much biologically valid assortative mating, for example, in fertility. The inheritance of fertility is for this reason perhaps less marked than in the outbred population or the Mennonites. Very fertile lines have appeared, however, in a few of the families. Among these it is worth noting (Mr Lucas tells me) that Don Alfonso of the Bourbon-Sicilies, who had forty-nine ggc, sprang from the same number of twelve ancestors

TABLE 13

Parallel marriage test in a homogeneous and fertile outbred family

C Rev. Richard Cockburn Kindersley (1831-71) *m.* Georgina Anne Kindersley (1838-1927) his first cousin.

U_1 His only brother
U_{2-6} His five male cousins
} married unrelated wives

M	Date	c				gc				ggc
		t	s	m	wi	t	s	m	wi	t
C . .	1857	11	10	7	5	13	12	9	7	18
U_1 . .	1852	12	11	7	6	27	...	...	...	...
	fraction traced*	...	...	...	...	14	14	9	8	13
U_{2-6} . .	1852-76	33	25	17	14	47	...	...	...	...
	fraction traced*	...	...	...	...	23	[illegible]	15	15	25
C cpm (wi) . .		11·0	45 per cent. passing tests			2·6	54 per cent. passing tests			2·6
U_1 cpm . . .		12·0	50 per cent.			4·5	57 per cent.			1·6
U_{2-6} cpm . . .		6·6	43 per cent.			3·4	66 per cent.			1·7

* From male children.

Notes: (i) This is the only cm recorded in the family since 1700.
(ii) Higher fertility is recovered in selected gc recombinants of cm.

Source: Mr Richard Kindersley, 15 Eccleston Square, London, S.W.1

TABLE 14

Sib marriage test in the progeny of a cousin marriage in a presumed inbred family

"White": *m.* 1870 his first cousin

c				gc				ggc
t	s	m	wi	t	s	m	wi	1
7	6 [1]	6	6	[illegible]	4	2	1	3+
				3 [2]	[illegible]	3	[illegible]	3
				4 [2]	4	3	3	17
				[illegible]	3	3	[illegible]	6
				1	1	1	1	2
				2	2	2	2	4+
				17	17	14	12	35+

[1] One daughter died: six sons survived.
[2] Parents again married first cousins.

Source: Anonymous.

equally in the 4th, 5th and 6th generations (*i.e.* 12/16, 12/32, 12/64, 22/128). And he married the daughter of an uncle-niece marriage of 1850. Similarly the present Comte de Paris, who is descended formally, although not genically, from Charlemagne in perhaps five million ways, has eleven children.

It seems likely that successful inbred groups (of which the Royal caste is merely a convenient and accessible example) have usually arisen not by a sudden adoption of inbreeding—such as we have seen with cousin marriage in our outbred families—but by a gradual contraction of their breeding group, as would happen at the beginning of all religious sects. Where the inbreeding has occurred suddenly there has been a great wastage of resources. Thus in the Ptolemies, the first full brother-sister marriage gave no surviving offspring. Their first successful inbreeding was a half-brother-sister marriage, which was followed by successful full brother-sister marriage.*

6. PARALLEL SIB-MARRIAGE TESTS

The parallel in- and out-breeding of sibs offers us the opportunity, as the Kindersley family shows, of making a more significant comparison than that between cousin marriages in different populations (table 13). Although some of the progenies are untraced, the remainder reveal the characteristic contrast in the results of the two types of marriage in an outbred stock.

A second parallel sib-test appeared in an inbred stock. The "White" family have been yeoman farmers in the Exeter district since 1600. They have been Nonconformist, some having been Plymouth Brethren. They should therefore have been subject to inbreeding. Their first known cousin marriage yielded as might be expected a uniform progeny both in viability and fertility (table 14). Of the six who survived all married and all had offspring. But two again married first cousins while four did not. The two inbreeders had twenty grandchildren; the four outbreeders had fifteen grandchildren with the possibility of a few more.

Here we have another indication (agreeing with table 2B) that inbreeding is more fertile in an inbred stock than outbreeding.

7. DOUBLE TEST MARRIAGES

We are now prepared to consider the most rigorous method that I have been able to use in studying the relation of fertility to the breeding system. Where a man or a woman has married in succession two spouses, one closely related and the other remotely related, or what is called "unrelated", we can often compare the numbers of descendants and their behaviour in each succeeding generation (table 15A-E).

* In this family, however, as in other ancient dynasties, too many princes were begotten and too many died in uncertain circumstances. Even the *mother* of the last Cleopatra is unrecorded.

TABLE 15

Double test marriages

A. Outbred Stocks

1. Ralph Sadleir, Canon of St Patrick's, Dublin (1815-1902) *m.* (i) 1839, Letitia Sadleir, first cousin (1818 ?-1867) ; (ii) 1871, Letitia Sewell, unrelated.

M	Date	c				gc				ggc
		t	s	m	wi	t	s	m	wi	t
C	1839	1	1	1	1	3	3	2	2	3
U	1871	1	1	1	1	1 [1]	...	...	...	...

[1] Burnt to death *c.* 1920.

Source : Colonel B. F. Trench of Halberton, Devon.

2. John Murgatroyd (1819-1876) of Howarth, Yorks *m.* (i) Elizabeth, unrelated 1820-1853 ; (ii) Mary Ann, first cousin, 1828-1896.

U	*c.* 1842	4	3	3	3	6	6	6	5	10
C	*c.* 1854	6	5 [1]	3	0	...	...	...	...	...

[1] All " eccentric but very alert ".

Note.—Robert Murgatroyd, father of John, was churchwarden to Patrick Brontë (1777-1861). The family was thus Church of England, a majority group. There were no previous known cousin marriages. It was also a prolific family, Robert having had 48 grandchildren including the ten in this table.

Source : Mrs S. E. Ryan, now in Dublin, a daughter of one of these grandchildren.

3. Anthony, 3rd Baron Henley (1825-1898) *m.* (i) Julia Augusta Peel (1826-1862), 1st cousin;[1] (ii) Clara Jekyll (1838:1922), unrelated.

C	1846	6	4	3	3	4	4	3	1	2
U	1870	3	2	2	2	9	11	8	7	23+

[1] The common grandfather of the cousin marriage was Sir Robert Peel, 1st Bt., father of the Prime Minister.

Source : The Hon. Michael Eden of Scaleby Castle, Cumberland ; Mr Eden has kindly determined the certain absence of cousin marriage for three generations prior to the cousin marriage in the Henley family and its probable absence in the Peel family.

4. Hugh (1830-1907) *m.* (i) unrelated wife (1877-1891) ; (ii) first cousin (1892-1907).

U	1877	2	2	2	1	1	1	1 [1]	1	6
C	1892	2	2	1	0	...	...	...	...	...

[1] Married three times.

Source : Lady Constance Malleson.

5. Constance Mary Saltan (1867-1948) *m.* (i) unrelated husband (1889-1898) ; (ii) first cousin (1898-1937).

M	Date	c				gc				ggc
		ı	s	m	wi	t	s	m	wi	t
U	1889	■	■	■	■	4	4	3	■	6
C	1898	■	1	■	...	...	...	...	...	...

Source : Miss Ann Wadham of Cambridge.

B. Intermediate (with previous cousin marriages)

1. Godfrey Wedgwood (1833-1905) (*cf.* table 7) *m.* (i) *c.* 1860 Mary Hawkshaw, *d.* 1863, unrelated ; (ii) 1879, Hope Elizabeth W., first cousin (daughter of cm).

U	*c.* 1860	1	1	1	1	■	2	1	1	■
C	1879	1	1	1	0	...	...	...	...	...

Source : The Hon. Mrs Helen Pease of Cambridge.

2. The Campbell-Callender Sequence

(*a*) John Henderson, *m.* Mary, first cousin, *c.* 1760.

C	6	6	6	4	13 [1]	1 [2]	1	1	14 [3]

[1] Some went to U.S.A. after 1798 rebellion ; all but one untraced.
[2] William Campbell of Derry, only child (1798-1862) on account of his father's emigration.
[3] Includes Thomas and Margaret Callender Campbell (*cf.* 2*b*) but not their cousin-spouses Thomas and Agnes Callender who were not descended from cm (see table 2A), *m.* 1858.

(*b*) Thomas Callender, *b.* 1836, *m.* (i) Margaret C. Campbell, first cousin *c.*1865; (ii) Mary McNab, unrelated, *c.* 1875.

C	4	3	3	■	6	5	2	2	5
U	5 [1]	4	2	2	6	■	4	4	14+

[1] Including twins.

Source : Dr Sheila Callender of the Radcliffe Infirmary, Oxford.

3. McLeod of Tain (1861-1925), *m.* (i) 1891, first cousin, daughter of presumed first cousins ; (ii) 1895, unrelated wife.

C	1891	2	1	1	1	4	4	4	4	8+
U	1895	2	1	1	0	...	...	...	...	...

Source : Mrs M. P. Close of Lone Cove, Sydney, Australia.

C. Inbred

(i) Non-Jewish

1. Count Watthier Hamilton (1783-1835), *m.* (i) Marie Helena v. Strokirch (1785-1820) unrelated ; (ii) Hedvig Hamilton (1800-1859), first cousin.

M	Date	c				gc				ggc
		t	s	m	wi	t	s	m	wi	t
U	1811	2	2	2	1 [1]	4	2	2	2 [2]	9 1
C	1821	6	5	4	3	1 4 4	1 4 4	1 4 3	1 [2] 4 3	9 16 9

[1] *m.* his first cousin, outside this pedigree.
[2] *m.* (being half cousins) and had gc, which are counted in each group.

Note. The repeated cms make comparison difficult in the third generation. The pattern of cm, however, continues the earlier habit of cm in this family as in Swedish nobility generally (*cf.* Alström, 1958; Fraccaro, 1958).

Source : Dr Per Selander of Malmö, Sweden.

2. *Double Test Marriage with a successive cm* : (i) H. A. v.d. Wall Bake of Amsterdam (1809-1874) ; (ii) A. M. A. v.d. Wall Bake (1852-1940).

1	C	1833	7	7	7	5 [1]	17	17	14	13	46
2	C	1877	2	2	2	2	6	6	5	4	14
	U	1884	3	3	2	1	4	4 [2]	3	3	9

[1] One of these is the husband in (2).
[2] One of these killed in war, unmarried.

Note. The twice-married spouse is himself of the first generation of a cm. His cm is thus a successive cm. Moreover, the families concerned belong to a closely inbred community with many previous cm.

Source : F. G. L. O. van Kretschmar of Westcott House, Cambridge.

(ii) Jewish (uncle-niece)

1. David—(1817-1886) Hanover, *m.* (i) Johanne—(1831-1867) unrelated ; (ii) Rachel—(1843-1924) half-niece.

U	1862	5 [1,2]	2 [3]	1	1	3	3	2	2	3
½N	1868	4 [3]	3	3	3	7 [4]	5	5	3 [5]	7

[1] Two died of tuberculosis.
[2] One stillborn.
[3] One died by suicide.
[4] One died at Auschwitz.
[5] *Propositus.*

Source : Anonymous, Montreal, Canada.

2. Hermann Wittner (1848-1926), Mischalenny, Roumania. *m.* (i) unrelated wife; (ii) niece (1858-1911).

M	Date	c				gc				ggc
		t	s	m	wi	t	s	m	wi	t
U	1872	3	3	3	1	2	2	0	...	...
N	1880	4	3	3	2	5	5	4	4	7

Source: Mr Frank Selby, of Hatch End, Middlesex.

D. Double Test Marriages

Non-first cousins

1. Johann Sebastian Bach (1685-1750), *m.* (i) Maria Barbara Bach (1684-1720), second cousin; (ii) Anna Magdalena Wicken (1701-1760) unrelated.

C_2	1707	7	3	2	2	6	3	0	...	...
U	1721	13	6	3	2	6	4	4	3	10 [1]

[1] 28 g^3c, 52 g^4c.

Source: C. S. Terry 1929; K. Geiringer, 1954.

2. James William Ardenne (1841-1921), *m.* (i) 1886, Emily Lane Harding (1846-1895), first cousin; (ii) 1898, his 1·5 cousin.

C	1886	2	2	1	1	1	1	0	...	...
1·5 C	1898	1	1	0	...	...	...	...	...	...

Source: Dr R. J. Hetherington, Birmingham.

E. Incomplete

1. Jens Paulson, of Fana, Bergen, Norway (1870-1953), *m.* (i) *c.* 1890, Anna Elizabeth, first cousin; (ii) *c.* 1910, Martha, Anna's niece, *i.e.* 1·5 c.

C	*c.* 1890	10	6	6	6	24	...	...	...	...
1·5 C	*c.* 1910	10 [1]	7	7	7	31	...	...	...	...

[1] One drowned.

Source: Dr John Harper, University of Oxford.

2. Engel ♀, *b.* in Hungary; *m.* (i) Siegmund Engel, 1887, first cousin and also uncle (mother's brother); (ii) Julius Ehrnfeld, 1902 unrelated.

C	1887	4	3	3	3	4	4	3	1	1+
U	1902	1 [1]	0	...	...	...	...	...	...	...

[1] Defective, mother aged *c.* 36 at his birth.

Source: Dr Eva Bene, London, W.1.

TABLE 15 (*Concluded*)

Summary of double test marriages

	1st M		Cousin			Unrelated			Ratio of increase
	C or U	Date	c	gc	ggc	c	gc	ggc	C : U
A. OUTBRED									
1. Sadleir	C	1839	1	3	3	1	1	...	
2. Murgatroyd	U	1842	6	...	...	4	6	10	
3. Henley	C	1846	6	4	2	3	8	23+	
4. Hugh —	U	1877	2	...	...	2	1	6	
5. Wadham ♀	U	1889	2	...	...	2	4	6	
Total			17	7	5	12	20	45	*0·3 : 3·7*
B. INTERMEDIATE									
1. Wedgwood	U	*c.* 1860	1	...	...	1	2	2	
2. Callender	C	1865	4	6	5	5	6	14+	
3. McLeod	C	1891	2	4	8	2	...	...	
Total			7	10	13	8	8	16	*1·9 : 2·0*
C. INBRED									
(i) *Non-Jewish*									
1. Hamilton	U	1811	6	9	34	2	4	10	
2. v.d. W. Bake	C	1877	2	6	14	3	4	9	
(ii) *Jewish* (*uncle-niece*)									
1. David —	U	1862	3	7	6	4	3	3	
2. Wittner	U	1872	4	5	7	3	2	...	
Total			15	27	61	12	13	22	*3·4 : 1·8*
Grand total: A, B, C			39	44	79	32	41	83	*2·0 : 2·6*
D. NON-1ST COUSINS									
1. Bach (2 C : U)	2 C	1707	7	6	...	13	6	10	
2. Ardenne (C : 1·5 C)	C	1886	2	1	...	1	...	...	
E. INCOMPLETE									
1. Paulson (C : 1·5 C)	C	1890	10	24	?	10	31	?	
2. Engel ♀	C	1887	4	4	1+	1	...	...	

There are four special points that need to be considered in attempting to apply this test.

First, the capacity to produce first generation children is not at issue. We must therefore compare the descendants of similar numbers of children, or per child.

Secondly, the number of children are likely to be small and unequal in the two families. In one case of the Engel family (table 15, E 2) I had to exclude the family since the sole child of the second marriage was possibly a mongolian type in which the mother's age was the significant factor. I have accordingly also stated in the summary which of the two marriages was the first.

Thirdly, we must divide our families into classes: those that have had no previous inbreeding or likelihood of it, and those that are derived from small social or religious groups that are known to have inbred. In practice, as we have seen, intermediate conditions where inbreeding is beginning give highly diverse results and must therefore be put in an intermediate class.

If we do not make this distinction the grand total of the progenies shows no significant difference between the effects of in- and outbreeding. When we make the distinction according to the antecedents of the families, however, we find that outbreeding favours the outbreeders and inbreeding favours the inbreeders. Further, these differential effects which are apparent in the numbers of grandchildren are exaggerated in the numbers of the great-grandchildren. They are proportionately exaggerated in the extreme example of outbred class A. This effect again suggests, as in table 2A, assortative mating in respect of fertility.

Apart from the Engel family, the non-first cousin and incomplete progenies in table 15 D and E, all seem to be from outbred stocks. But since, as tests, they are less significant, detailed enquiries on antecedents have not been made. The Bach family, however, is known to have had no previous cousin marriage. The extinction of the second cousin marriage line and the continuance of the outbred line is historically the most notable case of its kind.

8. INERTIA AND INNOVATION

On my interpretation it now seems that human stocks can maintain not only their greatest uniformity but also their highest fertility with regular cousin marriage. Indeed, the change to inbreeding provides the best means of selecting for high fertility. But the introduction of inbreeding in an outbred stock leads to loss of uniformity, viability, fertility, and total reproductive potential. This last effect often extinguishes a line in the second generation, or, owing to assortative mating, in the third or fourth generation, after a cousin marriage.

The method of dividing the population into inbred and outbred stocks and the further method of using parallel and double test

marriages has indicated a converse principle. This is the principle that outbreeding in an inbred stock, as compared with continued inbreeding, may likewise have a depressing effect on fertility. This inference should be tested with selected results recorded like mine over several generations. The most obvious fields are race crosses (such as Jewish-Christian crosses) and class crosses (such as the morganatic marriages of Royal families.

Following both types of change in the breeding system we may expect what we find in the first, namely that recombination gives lack of uniformity so that, following depression, a few recombinants will establish lines with increased reproductive potential.

These conclusions conform with certain observations reached on very different grounds. For example, considering heterosis in *Drosophila*, Dobzhansky (1950) concludes that inversion heterozygotes derived from crosses between races may fail to show the advantage that appears in such heterozygotes within a race. Vetukhiv (1954) has inferred an " integration " of the genotype from similar observations. On the other hand, in plants, a change in the breeding system, a shift to inbreeding, has been shown to lead to specific responses. In *Campanula* and *Œnothera*, following heavy selective elimination, it can change the direction of evolution so as to favour the establishment of altogether new genetic systems such as permanent hybridity (Darlington, 1956*a*, table 27).

These different kinds of reaction have been taken to imply an " inertia " in all genetic systems (Darlington and Mather, 1949; Mather, 1955). The present observations seem to bear out such an assumption, and it deserves to be fully explored in man as elsewhere. At the same time, however, other principles seem to be disclosed by the present treatment.

The cost of overcoming inertia, the loss of reproductive potential in the generations following a change of breeding system, usually extinguish all but the more fertile lines. But experience shows that it is by just this kind of change that the great innovations in evolution come about. The most successful breeders of cultivated plants have obtained their success, as I have shown in some detail (1956*b*) by changing the breeding system. The same is true of animal breeding, although here the inbreeding side is better known than the hybridisation, being more recent. So also it must be with man.* Out of the homogeneous, conventional, mediocre, well-adapted mass, recombination will bring new unbalanced types, usually defective, and eccentric, but also sometimes original, usually infertile but sometimes fertile and occasionally creative in both mind and body.

The loss of reproductive potential means the production of very large numbers of unsuccessful types accompanied by very small

* The effects of irradiation may be used as a less satisfactory substitute for a change of the breeding system. The analogy with loss of reproductive potential, rare advantageous effects and dependence on recombination is obvious (*cf.* Bruce Wallace, 1957).

numbers of successful types. These types are distinguished mostly not by specific genes but by specific combinations or systems of genes, chiefly of the order of polygenes but no doubt at all levels of gene evolution; usually fragile but sometimes persisting. The process which differentiates between the successful and the unsuccessful types is one of natural selection. The selective advantages concerned are preposterously high, if indeed one can speak of such relations where simple alternatives no longer exist. In this selection the observable character-differentials of classical genetics (or eugenics) are swept along by the overpowering force of the unobservable viability and fertility differentials. The analytical materials and their selective values are trivial in comparison with the rapidly evolving integral effects.

One limitation of these integral or combination effects needs to be noted at this point. They are of value, sometimes only in individuals, sometimes only in small breeding groups; very rarely perhaps are they of value when indefinitely extended. The reason for this is plain. It is that their selection is not bound to concern the individual's relation with his environment. It is bound to concern an integration of the genotype, which is an internal matter: it is, like what we call " personality ", an internal integration. The opportunity for external re-adaptation is, however, likely to be taken at the time when the internal re-integration is taking place, since changes in the breeding system in plants and animals and also in man usually arise together with—or even as a result of—changes in the external situation.

In this work of re-integration following a change of the breeding system, assortative mating is shown to be important by our enormous divergences in fertility in the second and third generations. It is therefore worth while recalling the origins of this idea.

Pearson and Lee (1903) having found a possible correlation between husband and wife in height of 0·28, Pearson (anonymously) makes certain novel remarks about sexual selection and about preferential and assortative mating. He points out that assortative mating with positive correlation between mates (which he calls homogamy) as opposed to random mating should have a contrast of effect almost as important as that arising from self- as opposed to cross-fertilisation in plants. He adds that assortative mating, however: (i) may have any degree of intensity; (ii) may be confined to special characteristics; (iii) need have none of the " harmful effects " of inbreeding. Even today, however, we still do not know how far assortative mating in man may not imply inbreeding in respect of particular genes or gene combinations or segments of chromosome.

This question is already raised in my attempt to relate cousin marriage to group inbreeding. It will, I believe, become important at a later stage in the study of breeding systems in man.

9. THE ORIGIN OF REGULATED OUTBREEDING

In sexually differentiated organisms, both sessile and mobile, both plants and animals, self-fertilisation is excluded, and this is the whole means by which inbreeding is directly limited. To this rule man is the sole exception. The rule and its breaking are therefore of vital importance for his evolution. He has adopted conventions which discourage or prevent sib-mating and even all mating within a wide range of kindred. All races of men that have survived today share these conventions. Their results are closely parallel to the similar systems arising in hermaphrodite plants (Darlington, 1943*b*). Both have to depend on the recognition of kinship. But whereas the recognition of kinship in a plant depends on its genetics, physiology and biochemistry, in man it depends on the special intellectual and cultural apparatus which he has recently evolved. How does it work?

This question has been asked more and more often since MacLennan first used the term exogamy in 1865. Many answers have been given. A few of these answers have rested on biological grounds. During his life, Darwin's explanation (1876) that outbreeding, as opposed to inbreeding, enhanced vigour or avoided debility in the offspring, or even the posterity, generally carried weight. But this belief, even at the time, could be seen to be mistaken and my evidence helps to show what the mistake was and how it arose. Fertility over several generations is a stricter test than viability in one generation. And fertility is as compatible with close inbreeding in man as it is in other animals or plants.

Most answers, however, have rested on no biological grounds at all. They have rested on arguments from purely human properties of custom, religion or fancy. The arguments attempted to explain what their authors did not understand, the biological property of outbreeding, in terms of what nobody understands, the local origins of human superstition. Explanations by Herbert Spencer, Frazer, Freud and others, therefore, run in smaller and smaller circles. These have been well described by Lord Raglan but even he has added his own magical formula to the series.

The most recent is of larger scope and deserves special mention. It is that of Lévi-Strauss (1949). This distinguished anthropologist states his conclusion at the beginning in the following words:

> "La prohibition de l'inceste . . . constitue la démarche fondamentale grâce a laquelle, par laquelle, mais surtout en laquelle, s'accomplit le passage de la Nature à la Culture." (p. 30).

Thus Lévi-Strauss by stating the fact three times (a fact which no one disputes) seems to persuade himself that he has explained the fact. This is just what he avoids doing. He has to avoid explaining it because he is unwilling to make any genetic assumption.

Now we know, however, that the long-term properties of genetic systems are themselves genetically controlled. We know that in all organisms they are subject to selection and evolution. And we know—this arises from the last thirty years' work—that wherever the long-term selective advantage can be traced it is the same: it is the securing of recombination and hence of adaptability in the population, and the securing of this sequence of advantages by outbreeding (Darlington, 1958*a*).

Outbreeding in all sexual organisms is only secondarily important for its immediate individual effect of avoiding homozygosity. Primarily it is important for its enduring population effect of exploiting heterozygosity. That is for combining lack of variation in a breeding group with the capacity to release variation when the breeding group either contracts or expands: which it does whenever conditions change; whenever, that is, they become unfavourable.

Enforced outbreeding therefore at once gives any population which knows how to adopt it an advantage over those which do not, the advantage of rapid adaptability. A change to inbreeding in such a population at once splits it into dissimilar groups, each homogeneous but with a homogeneity from which there is no return.

In these terms we can now see what happened at a certain stage in the evolution of man. As families stayed together longer, and as an intelligent recognition of kindred developed with discrimination, there would also develop that assortative mating which in man is peculiarly an intellectual gift. Groups would become more and more inbred, unadaptable and fissiparous. Large, homogeneous, co-operative groups could come into existence only when the gift of recognition of kindred was exploited to enforce the avoidance of mating with kindred. The recognition of kindred would therefore lead to a *breeding crisis*. The groups that survived would be those which had used their new gift to develop a system of outbreeding. The behaviour of primitive peoples throughout the world shows that they are all descended from such groups.

Regulated outbreeding not only limits inbreeding; it also limits or even abolishes assortative mating. For the regulation is often elaborate enough to leave no choice of mates. In both of these ways it tends to maintain a phenotypic homogeneity in the group. This homogeneity makes possible the cohesion without specialisation, the conformity with tradition and continuity, characteristic of tribal life. When the breeding system changes, this character breaks down and we have " detribalisation ". The breeding system is thus necessary in maintaining the adaptation of the primitive community not only externally to its environment, but also internally to its own parts as reflected in reproductive and cultural stability.

In selecting a genetic propensity for outbreeding in man nature therefore showed, not only a long-term preference for recombination, which we know to be universal, but also, as Tylor implied already in

1889, a short-term preference for social co-operation and initiative, which is peculiar to man himself.

If we imagine the contrary state, and indeed the pre-existing state of a society of baboons with no conventional restriction to mating at all, we can see what would have happened to it with man's developing intelligence. The tribe would be continually subject to splitting up by brother-sister mating into groups of irregular size and differing character just as happens in our own society to a less degree with inbreeding. Such irregularity would disintegrate tribal communities at the moment when intellectual processes began to affect mating habits.

The clumsiness, over-elaboration and occasional inefficiency or irrelevance of the rules which are connected with man's avoidance of inbreeding are of minor interest to the geneticist. He can see where they lose their aim. The complex of rationalisations and myths by which man has explained, justified and reinforced these rules, on the other hand, are characteristic of all his behaviour. They are of major interest to the anthropologist. He regards them as the genuine foundation of man's behaviour. But I am arguing that these ideas are secondary and derived. Derived from what? Derived always from instincts, from genetically determined systems of behaviour, selected for their long-term adaptive advantage and leading to an aversion for breeding between close kindred, an aversion for what at this stage we may call incest.

The instincts of a majority would establish social codes and mating taboos much on the lines proposed by Darwin in the *Descent of Man*. It would then be difficult and dangerous for diverging individuals to break the rules. Royal families could most easily do so, as they have done in varying degrees. The loss of the instinctive aversion to inbreeding also, we may note, runs in families. Does it do so for genetic as well as for merely imitative reasons? Consider the incest of Byron the poet, and of his father, each with a sister. The grandparents of all four were first cousins, and all members of the family who could marry first cousins did so. Is there a genetic component in this sequence? I believe so.

The third stage in the development of breeding rules is that where instincts pass into conventions, conventions pass into law, and it is worth noting that incest has been decreed a crime at many times in history. It was not, however, until 1908 that this stage in the organisation of the breeding system was reached in England, and it is a stage which may never be reached in other European countries. The position of homosexuality is analogous. Similar selective advantages must obviously operate against homosexuality and similarly give rise to moral precepts and legal sanctions. In both cases the precepts and sanctions have an instinctive basis; they are irrational and may be misguided.

The study of breeding behaviour and its effects in man on these lines helps us to disembarrass ourselves of a number of prejudices in

deciding on our future behaviour. It may help us to interpret the relations of instinct, reason and superstition where they are most entangled. The tribal breeding units, between whose instincts and hence customs selective processes originally distinguished, are now largely disintegrating. And in civilised societies the instincts are reduced to conventions supported by fallacious rationalisations. The long-term selective forces favouring adaptability in tribal societies are now superseded. All that is left is the evidence of what we may call instinctive residues, religious beliefs, and the secondary selective forces affecting individual survival. This evolutionary flotsam still gives stability to breeding systems. It also confuses the observer who confines his attention to man.

The parallel gifts for regulated outbreeding and for assortative mating, or outbreeding with discrimination, are, as I have suggested (1958*b*), the two inventions on which the evolution of human societies is based. They have been in a sense twin foundations; but rather more they have been connected and balanced foundations of his breeding system. They have made possible, first, the tribal society and, secondly, in the last ten thousand years, the class-differentiated society, the unprecedentedly rapid evolution of which we call civilisation. It is on their study that the future will also depend.

10. SUMMARY

1. In advanced societies taken as a whole a specific class of breeding (such as cousin marriage) shows no very pronounced departure from the average result in regard to any particular attribute of the progeny.

2. But when families are classified by their breeding system over several previous generations, and when all attributes are taken together as measured by the reproductive potential over several subsequent generations, decisive differences are found.

3. Inbreeders suffer by outbreeding and outbreeders by inbreeding. This is true on the average of each of the successive reproductive tests in the progeny: viability after birth, marriage frequency and numbers of the second generation.

4. These average effects are compatible with greater heterogeneity and the production of new strains, new recombinations, enhanced in fertility and no doubt often in other respects.

5. Assortative mating in respect of fertility, otherwise difficult to show, is to be inferred from the maintenance or exaggeration of these differences in successive generations.

6. The value of regulated outbreeding for primitive man was not in its avoiding homozygosity but in its providing homogeneity in an enlarged breeding group together with an immediate capacity for variation when the group changed either by contraction or expansion.

7. The origin of the regulation of outbreeding, it is suggested, was in the development of appropriate instincts on the lines proposed by

Darwin. This development would be favoured by their enormous long-range selective advantage on the principles of evolution in genetic systems as established in animals and plants generally.

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APPENDIX : ABBREVIATIONS

cm	first cousin marriage (three pairs of grandparents, one in common)
cm(d)	double cm (two pairs of grandparents, both in common)
cm(r)	reciprocal cm, of pairs with same three pairs of grandparents
cm(par)	parallel cm between pairs of sibs
cm(1·5)	first cm once removed
cm(2)	second cm
scm	successive cm, *i.e.* involving descendants of a cm after one or two generations
dtm	double test marriage

c	children
gc	grandchildren
ggc	great-grandchildren
t	total
s	survived to maturity (22-24 years)
m	married or marriage
wi	with issue
+	plus sign indicates that the possibility that more children will be born or discovered is not excluded
c & u	cousins/unrelated (of double marriages of one spouse)
cpm	children per marriage

FURTHER STUDIES ON THE EVOLUTION OF *MANIOLA JURTINA* IN THE ISLES OF SCILLY

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We have studied evolution in the butterfly *Maniola jurtina* (Satyridæ) since 1946. Part of the work has been conducted in the Isles of Scilly, and this aspect of it was last reviewed by Dowdeswell, Ford and McWhirter (1957) and by McWhirter (1957) in articles which carried it up to 1955. We are now describing it in the succeeding two years, a period during which new and decisive results have been obtained. These arise partly from the response of the *jurtina* colonies to the weather conditions of 1957, unprecedented in the Isles during our experience of them and no doubt long before, and partly from the more intense analysis of the insect upon the larger islands which it has now been possible to conduct.

As in the past, we make use of a quantitative character, the number of spots on the underside of the hind wings, for analysing the variability of this species and its response to differing conditions. The extreme stability of their frequency-distributions year by year in certain populations, and their power of rapid adjustment to ecological change in others, indicate that the genes which control spotting are of great selective importance. One of us (W. H. D.) has, moreover, already obtained experimental proof for this conclusion, the details of which will be published in the near future.

1. THE LARGE ISLANDS

Between 1950 and 1955 twelve large samples of female *M. jurtina* were taken on St Mary's, St Martin's and Tresco. We have tabulated the spot-distributions (Dowdeswell, Ford and McWhirter, 1957) and shown that they are homogeneous both from year to year and from island to island. This " large island " stabilisation was clearly as firm and as well-established as that of Southern England between the years 1950 and 1952, despite the fact that the three populations were isolated from one another by at least a mile of sea. All samples regularly showed the " flat-topped " distribution in which the proportions of females at 0 spot, at 1 spot and at 2 spots were approximately equal.

Even by 1954, however, a " second-order " distinction had begun

to appear between St Mary's on the one hand and St Martin's and Tresco on the other. The proportion of females at three or more spots has, from 1954 onwards, been regularly greater on St Mary's than on the other two islands, and the proportion of females at 1 spot very slightly less. If a comparison is made as in table 1, it will be seen that $\chi^2_{(4)} = 13{\cdot}84$; $0{\cdot}01 > P > 0{\cdot}001$.

Only large-scale and repeated sampling can be expected to bring second-order variations of this kind to light. We have even more intimate knowledge of the " large-island " stabilisation area than of any of the three principle types found on the mainland (that is, the South English, the East Cornish and the West Cornish), and its primary or first-order characteristic (the " flat-topped " distribution) which we have used to define it remains, of course, quite undisturbed.

TABLE 1

Comparison of female spotting on St Mary's and on the other two " large " islands, 1950-1955

Spots	0	1	2	3	4	5	Total
St Mary's 1951-55 . .	109	90	108	30	14	1	352
St Martin's and Tresco, 1950-55	412	387	398	67	23	1	1288

In 1956 the first sign of a break-up of this stabilisation could be seen on St Martin's and by 1957 the populations of the Main Areas of both St Martin's and Tresco had moved decisively away from the familiar " flat-topped " distribution, while on St Mary's, the largest island, a much reduced population maintained the same spot-ratios as before. In contrast to the surge of high-spotting which upset the South England stabilisation in 1955-57 (see Creed *et al.*, 1959) and reached its peak in 1956, the disturbance affecting the " large island " stabilisation produced low-spotting in the females and culminated in 1957. Reference to fig. 1, however, shows a general trend towards higher spotting in the males from 1955. Although on the mainland no ecological factor could be picked out as having caused changes in selection-criteria, in Scilly the disturbance of the female spot-distribution was clearly due to a number of factors, chief among them drought, which contributed to an acute shortage of grass.

The changes in the *M. jurtina* populations of the large islands are presented in diagrammatic form in figs. 1 and 2, and are also summarised in tables 2 and 3.

It is now necessary to take each island separately and to record *seriatim* the more intimate details of the ecology and of the estimated population size, before going on to consider the disruption of the stabilisation in general and the light it throws on population dynamics.

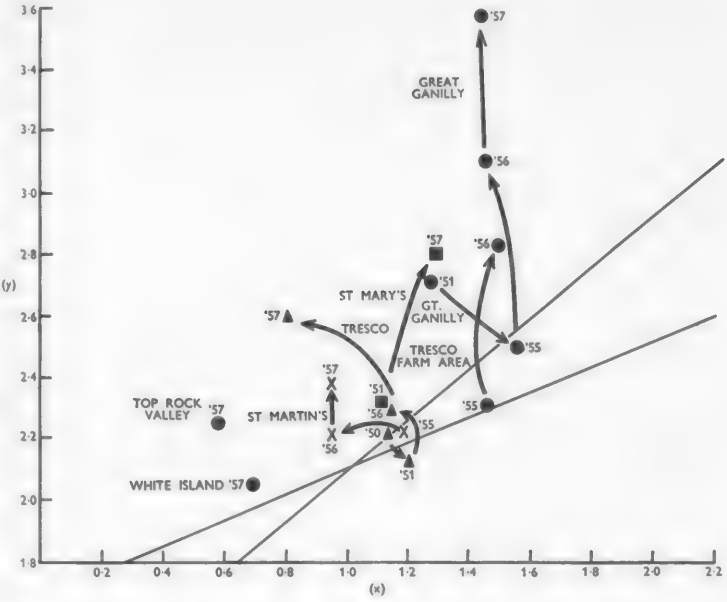

FIG. 1.—The correlation of male (y axis) with female (x axis) spot-averages in some Isles of Scilly populations of *M. jurtina*. The regression lines are based on all the data obtained from the Mainland and Scilly between 1946 and 1955 (McWhirter, 1957, fig. 1).

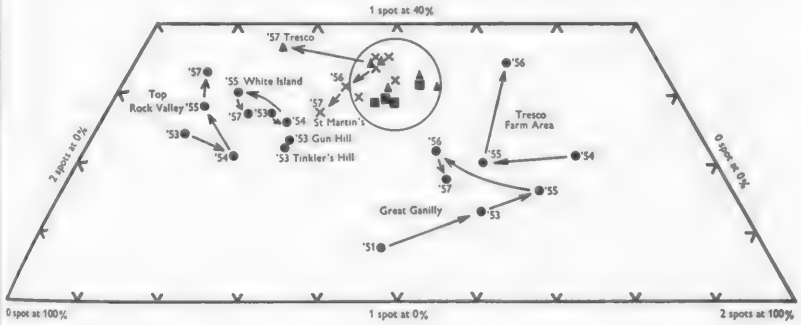

FIG. 2.—Triangular graph showing the frequencies of female *M. jurtina* at 0, at 1 and at 2 spots expressed as a percentage of the total at 0, 1 and 2 spots (cf. McWhirter, 1957, fig. 2 and Appendix). All large island populations fell within the circle during the period of stabilisation between 1950 and 1955 (▲ Tresco ; × St Martin's ; ■ St Mary's ; ● small islands or enclaves of the large islands).

TABLE 2

Spot-numbers of the large island populations of M. jurtina *in 1956 and 1957*

Island and year	St Martin's 1956	Tresco 1956	St Martin's 1957	St Mary's 1957	Tresco 1957
Males					
■	■	1	1	...	1
1	10	5	6	...	...
2	71	47	29	4	6
3	21	21	19	4	5
4	7	1	3	1	3
5	1	2	2	...	...
Total . .	111	77	60	10	15
Spot-averages	2·23	2·29	2·38	2·80	2·60
Females					
0	63	34	73	15	21
1	49	30	42	12	17
2	43	34	42	14	1
3	6	5	10	6	2
4	...	2	...	1	...
Total . .	161	105	167	48	48
Spot-averages	0·95	1·15	0·93	1·29	0·81

TABLE 3

Summary of changes in large island populations, 1956-57

Frequency of *M. jurtina*	Ecological changes	Changes in female spot-distribution
St Mary's Area tenanted was reduced; numbers much lower.	Nothing obvious.	Nil; the 1957 sample conforms precisely with those of 1951-55.
St Martin's Area tenanted was reduced; numbers still high in some parts of the main area, but clear overall reduction occurred in 1957.	Trend towards reduction of grass first obvious in 1957.	Progressive shift to lower spot-average and to mode at 0 spot, during 1956 and 1957. By 1957 reversion to the alternative low-spot stabilisation, peculiar to this island, had occurred.
Tresco Area tenanted and numbers were drastically reduced in 1957.	Many remarkable changes involving catastrophic reduction in grass occurred in 1957.	The "flat-topped" stabilisation persisted in 1956, but there was a sudden and unparalleled reduction in high spot specimens in 1957.

(i) *St Mary's*

This island was not sampled in 1956 owing to commitments elsewhere, but, as table 2 shows, the "flat-topped" female stabilisation had been maintained into 1957. If the 1957 females are compared with the three samples obtained in 1951, 1954 and 1955 (table 4) and the expectations for the categories 0 spot, 1 spot, 2 spots, 3 and more than 3 spots, calculated, we obtain $\chi^2_{(3)} = 0{\cdot}14$; $0{\cdot}99 > P > 0{\cdot}98$. In fact, our sample of 48 females in 1957 could hardly have fitted the previous St Mary's distribution more exactly. So far as could be seen from the very small sample of males (table 2) which it was possible to collect, some increase in male spotting seemed to have taken place in 1957.

No obvious changes in the ecology of our collecting area were found but the general tendency throughout the southern half of Britain for the 1957 flying populations to be small was much in evidence.

TABLE 4

Comparison of the spot-distributions of female M. jurtina *on St Mary's 1951-1957*

Spots	0	1	2	3	4	5	Total
1951-55	109	90	108	30	14	1	*352*
1957	15	12	14	6	1	0	*48*

Shortage of time precluded any attempt to make an accurate estimate of the size of the population by the method of mark-release-recapture. We can only say that we devoted some ten net-hours on two days in excellent collecting weather and took no more than 48 females and 10 males. Such specimens as we found were mainly in good condition; there was no question but that emergence was continuing at least up to the end of August. Grassy areas which had swarmed with *M. jurtina* in 1955 were virtually untenanted. Although our estimate must be subjective, we had no doubt that a considerable reduction in numbers had occurred.

(ii) *St Martin's*

In 1956 an increase in the number of 0 spot phenotypes was observed in the females; this was not, when compared with the five samples of females taken in 1950-51 and 1953-55, a significant difference. Tables 2 and 6 give the relevant figures and $\chi^2_{(3)} = 3{\cdot}99$; $0{\cdot}3 > P > 0{\cdot}2$. However, we found that if the percentage of specimens at 0 spots, 1 spot and 2 spots were plotted on a triangular graph, then the datum (40·6 per cent.; 31·6 per cent.; 27·7 per cent.) fell for the first time just outside the small circle into which all previous "large" island data had fitted. Fig. 2, which is based on the percentage system described by McWhirter (1957), illustrates this. No obvious ecological

change had occurred on the island; it seemed that the alteration in spot-distribution might be a slightly exaggerated example of a tendency of the St Martin's population to develop a small and temporary increase in the 0 spot phenotypes, as had occurred in 1953 and 1955 (see also table 5). That this turned out not to be so will be seen from our analysis of the totals of St Martin's Main Area in 1957 on pp. 344-346.

Returning to the Isles of Scilly in 1957 we camped at the south-west corner of St Martin's and used this opportunity to explore the island more minutely than before. By dividing it into small sub-areas we were able to show that these stabilised populations are not mixtures of smaller, differentially adjusted sub-populations but are homogeneous between localities. These more intimate data are discussed and listed below at pp. 344-346 (table 10). Here it is only necessary to note the totals for the whole of the St Martin's stabilisation area (table 2) and to remark that, compared with 1956, the spot-averages had further declined and the mode at 0 spots in the females had markedly increased. The spot-averages are listed in table 5, and the datum for the main St Martin's stabilisation in 1957 is also entered in fig. 2. From this it will be seen that the shift in 1957 was a further departure from the normal " large island " stabilisation and continued the smaller movement recorded in 1956.

It may also be noted from table 2 and fig. 2 that the number of female specimens at 1 spot and at 2 spots was equal and that the main St Martin's datum for 1957 is not far from the two data for St Martin's " South-East " (the Gun Hill area) and St Martin's " North-West " (the Tinkler's Hill area) which were obtained in 1953. If the two female samples obtained in 1953 from these isolated enclaves and that taken from the main stabilised area of St Martin's in 1957 are compared, as in table 7, we find that they closely approximate, with $\chi^2_{(6)} = 2{\cdot}62$; $0{\cdot}9 > P > 0{\cdot}8$. Thus there is evidence that the genetic structure of the St Martin's population is such that in response to certain changes in selection-pressures it is able to develop an alternative stabilisation. This is of interest when it is recalled how the populations of the great South English stabilisation moved to two alternative spot-patterns, which in that case involved reduced modes of 0 spots, around the year 1955 (Creed *et al.*, 1959). We may characterise this " St Martin's alternative stabilisation " as one which produces a female spot-pattern with a mode of somewhat less than 50 per cent. at 0 spots, and with the 1 spot and 2 spot levels equal at somewhat less than 25 per cent.

It was an obvious task to try to collect samples from the two enclaves, Gun Hill and Tinkler's Hill (marked on fig. 3 as sub-areas " G " and " H " respectively), again. Unfortunately we encountered cold weather with high winds, which heavily reduced the flying population in the Main Area of St Martin's and prevented us catching a single specimen in the enclaves. If these were tenanted, however, it is probable that their populations were small.

Although we could detect no obvious ecological changes in the main area of St Martin's in 1956, the effects of the spring drought were apparent in 1957. They were not so drastic as those in the isolated Top Rock Valley area, described on pp. 348-350, but reduction, as opposed to destruction, of bramble was marked and rabbits appeared to be unusually common. Shelter from long grass and herbs was generally much diminished. Accordingly we supposed that the stabilised population on St Martin's, which had resisted all the climatic vagaries of the years 1950-55, had responded to the exceptional drought

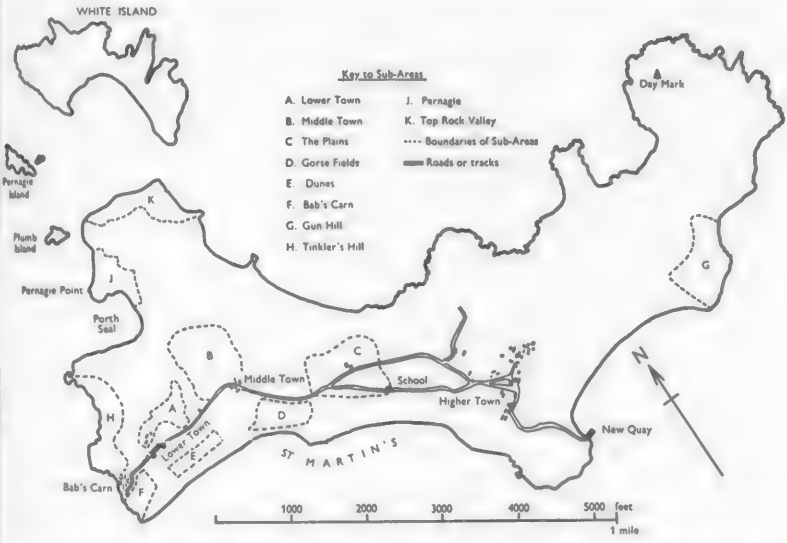

FIG. 3.—St Martin's and White Island, showing the boundaries of the collecting areas from which samples of *M. jurtina* have been taken. The samples recorded as St Martin's Main Area between 1950 and 1956 were collected in sub-areas B, C and D.

of 1956-57 by moving over to its alternative and lower-spotted stabilisation, so that if the 1956 and 1957 female samples are compared with those of 1950-55, $\chi^2_{(3)} = 8{\cdot}04$; $P < 0{\cdot}05$. (This and other comparisons are recorded in table 6.) As will be seen from pp. 344-346, all sub-populations of the Main Area performed this movement simultaneously.

A further interesting feature of the situation in St Martin's is that the male spot-average after remaining constant from 1950 to 1956 increased in 1957 when the female spot-average reached its lowest point. Such disturbances in the male-female correlation, which is normally a strong one (McWhirter, 1957), are often noted when a stable condition is upset and are of some theoretical importance (see p. 359).

(iii) *Tresco*

As reference to table 2 and figs. 1 and 2 will show, on Tresco, the third of the "large islands" which we have studied, no shift from the "flat-topped" female distribution was detectable until 1957. In 1956 the appearance of our main collecting area was quite normal. Yet the

TABLE 5

Changes in spot-averages of male and female M. jurtina *on St Martin's, Main Area, 1950-1957*

Year	Total male insects	Total spots	Male spot-average	Total female insects	Total spots	Female spot-average
1950	117	251	2·15	109	128	1·17
1951	293	652	2·23	116	127	1·09
1953	56	120	2·14	119	120	1·01
1954	...	...	...	237	264	1·11
1955	81	180	2·22	244	290	1·19
1956	111	248	2·23	161	153	0·95
1957	60	143	2·38	167	156	0·93

TABLE 6

Comparison of female M. jurtina *in St Martin's Main Area, 1950-55 with the 1956, 1957 and combined 1956-57 populations*

Spots	0	1	2	3	4	Total	
St Martin's Main Area 1950-55	*272*	*251*	*247*	*41*	*15*	*826*	$\chi^2_{(5)} = 3{\cdot}99$; $0{\cdot}3 > P > 0{\cdot}2$
St Martin's Main Area 1956	63	49	43	6	...	*161*	
St Martin's Main Area 1957	73	42	42	7	3	*167*	Compared with 1950-55 $\chi^2_{(5)} = 7{\cdot}15$; $0{\cdot}10 > P > 0{\cdot}05$
St Martin's Main Area 1956-57	*136*	*91*	*85*	*13*	*3*	*328*	Compared with 1950-55 $\chi^2_{(5)} = 8{\cdot}04$; $P < 0{\cdot}05$

TABLE 7

The alternative lower-spotted stabilisation on St Martin's (female M. jurtina, *1953 and 1957)*

Spots	1957 Main Area	1953 N.W. Enclave Tinkler's Hill (H)	1953 S.E. Promontory Gun Hill (G)	Totals
0	73	51	55	*179*
1	42	21	24	*87*
2	42	24	27	*93*
3 and >3	10	7	4	*21*
	167	*103*	*110*	*380*

$\chi^2_{(6)} = 2{\cdot}62$; $0{\cdot}9 > P > 0{\cdot}8$.

ecological change which had occurred by August 1957 was the most marked and extensive we have ever seen in the Isles of Scilly. We are convinced that it is not coincidental that the shift between the female spot-distribution of 1956 and that of 1957 is also the most remarkable recorded, not only on the large islands of Scilly but in any population of *M. jurtina* so far.

The most outstanding feature of the ecological situation in the Main Area of Tresco in 1957 was the dearth of grass. Very large stretches of former grassland had been swallowed up in an invasion of *Carpobrotus edulis*. This succulent herb (better known under the names " Mesembryanthemum " or " Hottentot fig ") seems to be a garden escape; it originates from South Africa. *C. edulis* produces a strongly growing tussock of thick, fleshy leaves with occasional yellow flowers. Grasses are smothered by it.

Mr J. E. Lousley (personal communication, 1958) kindly informs us that *C. edulis* " can establish itself in the open on the south coast as far east as Seaford and by comparison with this it seems unlikely that any frost Scilly has experienced recently would affect it very seriously. *C. edulis* has been established in Scilly for nearly 50 years and my own impression over the last 20 years is that it has increased fairly steadily except for more rapid increases of a local nature following fires. . . . droughts favour an increase in *Carpobrotus*, and there have been several severe droughts in recent years. Conditions in May and June last year, 1957, may well have favoured rapid elongation of the stems while bracken was short and gave little shade. My notes over the last few years repeatedly refer to bracken only a foot in height in places where it was formerly much taller."

Apart from the sudden increase in the rate of spread of *Carpobrotus* in Tresco, other factors still further reduced the grass crop in 1957. First, the population of rabbits in the collecting area seemed, judged by fæcal traces, to have increased enormously. Secondly, as elsewhere in Scilly, bracken and bramble died back. On one slope facing the western shore, there was, up to 1956, a flourishing population of *M. jurtina*, which was, however, difficult to catch owing to the tangle of brambles, which allowed many specimens to escape the nets. In 1957, it was possible to walk through the much reduced bramble clumps without hindrance, but not one specimen of *M. jurtina* was to be seen there. Poor as the grass was, it is unlikely that starvation reduced the numbers of *M. jurtina*. In a normal year, rabbits do not graze among bramble clumps, and it seems that the relatively lush grass around them affords not only food but perhaps protection from predation to larvæ. In 1957, however, all the grass was nibbled right up to the centres of the stunted brambles. Increased selection, rather than absolute starvation, seems a more likely reason for the drastic reduction in the flying population of *M. jurtina*.

The result of all these changes was that within a year what had been a reasonable and diverse feeding-ground for *M. jurtina* became a

restricted semi-desert: only short, poor grass remained. For the insect the habitat was, in 1957, bleaker than any of the windswept areas of White Island or the adjacent part of St Martin's. We have stressed the suddenness of the ecological crisis because it appears to us to explain precisely why selection has operated so strongly against the high-spot specimens (see table 8). With great difficulty and the expenditure of twenty net-hours spread over two days of fair to perfect collecting weather we obtained no more than 48 females and 15 males, the majority of which were perfectly fresh and had obviously only recently emerged. The population in this area has never been dense, but up to 1956 we had generally collected 100 females at the expense of ten net-hours and many more specimens were seen but escaped in the more densely vegetated areas. In 1957 nearly every specimen seen was caught.

TABLE 8

Distribution of spot numbers in female Maniola jurtina
Tresco, Main Area, 1950-1957

Spots	1950-56	1957
0	174	21
1	166	17
2	185	8
3	31	2
4	10	...
5	1	...
Total . . .	567	48

The spot-distribution data in *M. jurtina* seem clearly to indicate that the intensity of selection on Tresco has been greater than on St Martin's. On Tresco a catastrophe seems to have overtaken a large and stable population and to have selectively eliminated the high-spot specimens at a late stage in their life-cycle (for the drought was most intense during May and June). The percentages of the Tresco females at 0 spots, 1 spot and 2 spots are now 46 per cent., 37 per cent. and 17 per cent., so that the datum for 1957 has shifted decisively into the low-spot category, as can be seen when it is plotted in fig. 2. The high reading of 37 per cent. for 1 spot is unprecedented and probably indicative of exceptionally strong disturbance.

It is important to develop a method of estimating the statistical significance of this selective elimination of the more highly spotted female specimens in 1957. From table 8 it can be seen that, if this 1957 sample is compared with the homogeneous " flat-topped " samples obtained between 1950 and 1956, we obtain $\chi^2_{(2)} = 7{\cdot}19$, with P just exceeding 0·02. (The small size of the 1957 sample makes it necessary to group the data for 2 and more than 2 spots.) It also seems clear that no significant selective elimination took place in 1957 against specimens

at one spot. If we combine the data for 0 and 1 spot we obtain $\chi^2_{(1)} = 6{\cdot}10$; $0{\cdot}02 > P > 0{\cdot}01$, using Yates' correction.

These estimates of heterogeneity, while establishing that a highly significant change took place, are based merely on the abnormal distribution of the 1957 sample. In the biological context, however, we know that a number of high-spotted females which we " expected " to catch in 1957 were not caught (nor even, probably, seen).

Reducing the data to the 2×2 form, as in table 9, it appears that the relative frequency of the high-spotted specimens in 1957 was $\frac{ad}{bc} = \frac{10}{227} / \frac{38}{340} = 0{\cdot}394$. Woolf (1954) has described a convenient method of estimating fiducial limits of the function $\frac{ad}{bc}$, which he terms x. Applying this technique to ascertain the 95 per cent. confidence limits we find them to be 0·193 and 0·807.

TABLE 9

Data of table 8 reduced to a 2×2 table

Spots	1950-56	1957
0 and 1 . . .	340 (*a*)	38 (*c*)
2 and more than 2 .	227 (*b*)	10 (*d*)
Total . .	567	48

The same result can be reached intuitively after a consideration of the biological situation. On the null hypothesis that no selective elimination of the high-spotted females was taking place, we should have expected to catch $\frac{227}{340} \times 38 = 25{\cdot}4$ insects in this category in 1957. Since in fact 10 such specimens were caught the deficiency was $25{\cdot}4 - 10 = 15{\cdot}4$, and the percentual elimination was $\frac{15{\cdot}4}{25{\cdot}4} \times 100 = 60{\cdot}6$ per cent. Algebraically this estimate is:

$$\frac{\left(\frac{b}{a} \times c\right) - d}{\left(\frac{b}{a} \times c\right)} = 1 - \frac{ad}{bc} = 1 - x.$$

Again applying Woolf's method, the selective elimination of high-spotted females in 1957 was 60·6 per cent. with 95 per cent. fiducial limits at 80·7 per cent. and 19·3 per cent. This calculation allows for sampling error in all four cells of the 2×2 table, but since virtually the whole flying population was netted on two days in 1957, one of the sources of sampling error may have been diminished in that

year, so that intuitively one may be led to the conclusion that the 95 per cent. fiducial limits are not so wide as those estimated above.

This is the strongest selection pressure against a group of widespread phenotypes in a variable wild population that has ever been recorded. We cannot as yet, owing to the difficulty of pairing *M. jurtina*, offer any precise suggestions as to what such high selective elimination during one generation of the high-spotted female phenotypes may mean in terms of gene-frequencies, but since there is evidence from population data that spot-numbers are closely governed by the genotype, we should expect to see some signs of the 1957 crisis in later samples which we hope to obtain from the Main Area of Tresco.

It is also of importance to note that while the females on Tresco suffered a heavy reduction in spot-average in 1957, the males, on the contrary, so far as we can judge from a rather small sample, became more high-spotted than before (see table 2). The male spot-average in 1956 was 2·33, which is higher than usual for the large-island populations, while in 1957 it reached 2·60 (see fig. 1).

(iv) *Local homogeneity of the population in St Martin's (Main Area)*

In 1957 we attempted for the first time to analyse one of the stabilised large-island populations in detail. We had for long felt that, except in places where isolation was constant and effective, the large islands supported a population which was adapted to the general mixed ecology of the extensive habitat and had developed an appropriate genetic structure (Dowdeswell and Ford, 1953). Nevertheless, we decided that we should test the possibility that our large-island stabilisation might be composed of a mixture of insects derived from a number of relatively isolated habitats, each of which had developed a specialised population, some with modes at 0 spots and some with modes at 2 spots.

To obtain further evidence for or against the hypothesis of mixture, we divided the Main Area of St Martin's into six sub-areas, following boundaries which separated regions of different cultivation and of different natural ecology so far as possible. The approximate limits of the six sub-areas are recorded in fig. 3. Our 1957 sample was registered with reference to these sub-areas, except that on one occasion we mixed small samples from Lower Town and from Middle Town after it had become apparent that the two gave homogeneous results. The breakdown of the sample from the Main Area of St Martin's into sub-areas is recorded in table 10.

The characteristics of the sub-areas are as follows:

"A" *Lower Town*. This sub-area stretches from the cluster of houses called Lower Town up to the crown of the west end of the island. The land is mostly devoted to small bulb fields, covered in summer with grass and herbs, and usually surrounded by wind-breaks of *Pittosporum* and *Veronica* exceeding ten feet in height.

M. jurtina was more abundant here than in any other place on the large islands which we visited in 1957.

"B" *Middle Town.* This sub-area is more exposed than "A". It forms a horse-shoe round a deep cleft running from Middle Town up to the crown of the west end of the island. The land is less intensively cultivated than that of sub-area "A"; the higher parts are covered with bracken and bramble.

"C" *The Plains.* Sub-area "C" occupies the Plains, an exposed plateau above Middle Town. Even here, however, there is some shelter from the wind in lanes and dells covered with bramble and bracken. Half of this sub-area lies on the south side of the road, which forms no barrier to the insect. Parts of "C" which had swarmed in recent years with *M. jurtina* to such an extent that three or four specimens were often in the net together, carried very small populations in 1957.

TABLE 10

Breakdown of St Martin's Main Area population of M. jurtina *into sub-areas, 1957*

Sub-area	Spots						Total
	0	1	2	3	4	5	
Males							
"A" . .	...	2	4	3	1	...	10
"B" . .	1	1	8	6	1	1	18
"C" . .	...	3	17	[illegible]	...	...	28
"A"+"B" .	...	...	...	[illegible]	1	1	4
Females							
"A" . .	26	10	12	[illegible]	...	...	50
"B" . .	27	22	17	2	[illegible]	...	70
"C" . .	16	8	10	3	1	...	38
"A"+"B" .	4	2	3	...	...	...	9

"D" *Gorse Fields.* This sub-area lies south and west of "C" and wholly on the south side of the road. On the east it is composed mainly of fields which have gone out of cultivation and now contain large clumps of gorse. Towards the west it fades into the sand-dunes which line the south coast. "D" has been very well populated with *M. jurtina*, but not one specimen was caught there in 1957.

"E" *The Dunes.* This sub-area lies along the south coast to the west of "D". No insects were caught here in 1957.

"F" *Bab's Carn.* This sub-area occupies the south-western corner of the island and is dominated by Bab's Carn, a prominent rock which forms the north-western boundary. It seems to be isolated from the rest of the island by the buildings of Lower Town to the north, by the sea to the south and west, and by highly cultivated fields and unoccupied sand-dunes to the east.

We calculate that the female populations of sub-areas "A", "B" and "C" are substantially homogeneous ($\chi^2_{(4)} = 3{\cdot}68$; $0{\cdot}5 > P > 0{\cdot}3$). Sub-area "F" (see table 11), when compared with sub-areas "A", "B" and "C" grouped together gives $\chi^2_{(2)} = 3{\cdot}49$; $0{\cdot}2 > P > 0{\cdot}1$. Thus it does not differ significantly from the rest. However, in view of the apparent deficiency of female specimens at 1 spot and of the fact

that this sub-area may be isolated and has not been previously sampled, we have excluded it for the time being from the Main Area of St Martin's (see table 11).

From the results of the sampling of sub-areas "A", "B" and "C", we are satisfied that the large island stabilisation does in fact represent a genetic condition evolved as a response to mixed ecology. Thus it appears that all parts of the Main Area of St Martin's, now defined as being composed of at least sub-areas "A", "B" and "C", have taken part simultaneously in the shift to the alternative, lower-spotted stabilisation.

TABLE 11

Spot-frequencies of M. jurtina *in St Martin's Area "F"*
(*see p. 345*)

Spots	0	1	2	3	4	5	Total
Males .	...	...	3	1	2	1	7
Females .	9	2	9	1	...	...	21

2. ISOLATED AREAS ON LARGE ISLANDS

(1) *The "Farm Area"*

If, as we believe, the uniformity of female spotting on the large islands in Scilly has developed in response to the average of the diverse conditions existing on them, we might expect any small isolated population to achieve a local adjustment differing from that of the island as a whole. One such colony was found on Tresco in 1954, occupying 200 × 70 yards of rough ground (the "Farm Area"). This was used by the Royal Navy during the 1914-18 war and huts were built upon it. Their concrete foundations remain and around them has grown up rank vegetation of a highly exceptional kind, mostly garden escapes unsuitable as food for *jurtina*. The site, which included pigsties in 1955 and 1956, is bounded to the north by estate workshops and a village, to the west by the shore and to the east by a road and hedge bordering a narrow strip of grass beyond which is a lake. Southwards, between the sea and extensive pine woods, is a tract of bracken, bramble and very short turf; *M. jurtina* cannot colonise this type of habitat, but a path leading to the main collecting grounds of the island traverses it. This may provide a passage for the insect, but no appreciable flow of the butterfly has been observed here even when it was quite plentiful.

The colony inhabiting the Farm Area, totalling no more than 100 to 150 flying insects, was studied in 1954 and 1955 (Dowdeswell *et al.*, 1957). The spotting of the females was similar in the two years

and differed significantly from that of the colony inhabiting the main part of Tresco, which had itself remained constant not only during that time but since first examined, in 1950.

On visiting the area in 1956 we found the ecology somewhat changed. A field bordering the path running south from it, which had previously supported a dense growth of Red Campion (*Melandrium dioicum*), was now ploughed and sown with grass. *Maniola jurtina* was flying freely here, suggesting the possibility of a leakage from the Main Area of Tresco. This was tested by marking as many of the "Farm Area" population as could be caught in a single day (35 males; 36 females). A subsequent sample collected six days

TABLE 12

Female spot-distributions of M. jurtina *in two areas on Tresco*

Spots	0	1	2	3	4	Total	Homogeneity
Farm Area							
1954 . . .	5	6	18	6	0	35	$\chi^2_{(6)} = 4{\cdot}064$
1955 . . .	23	16	40	6	4	89	$P > 0{\cdot}5$
1956 . . .	6	11	15	3	1	36	
Total . .	34	33	73	15	5	160	
Main Area							
1954 . . .	26	28	36	5	1	96	$\chi^2_{(6)} = 5{\cdot}428$
1955 . . .	32	31	27	7	4	101	$P = 0{\cdot}5$ approx.
1956 . . .	34	30	34	5	2	105	
Total . .	92	89	97	17	7	302	

Difference of Farm Area from Main Area : $\chi^2_{(3)} = 13{\cdot}816$, $0{\cdot}01 > P > 0{\cdot}001$.

later included no marked specimens but a high proportion of completely fresh insects of both sexes, which indicated either local immigration or emergence. The fact that spotting in the females proved to be different from that of the only region whence immigrants could have come, demonstrates the latter alternative.

Table 12 shows that throughout 1954-56 female spotting in the Farm Area remained unchanged but differed significantly from that in the Main Area of Tresco, which had also remained constant throughout that period. Thus the spot-frequencies indicate that the insect was responding to exceptional conditions in a restricted and isolated habitat. To this it had become stabilised by selection powerful enough to overwhelm any action of random drift and any influence due to immigration.

On revisiting the area in 1957, it was at once apparent that great changes had taken place since the preceding year. The pigsties which formerly occupied part of the locality had been removed, leaving a patch of denuded earth. The small amount of grass had been almost

entirely replaced by a dense mat of *Carpobrotus*, with the exception of a few square yards in the north-eastern corner where two *Maniola jurtina* were found. In all, a search of four net-hours revealed only 4 insects (all females), 2 at 0 spots, 1 at 2 spots and 1 unscorable, and it was clear that the population of the Farm Area had been reduced to an extremely low level.

(ii) *Top Rock Valley (formerly referred to as the coastal area of St Martin's opposite White Island)*

Reference to fig. 3 shows a strip of the north-west coast of St Martin's about 500 yards long and up to 100 yards wide (marked as sub-area " K "). Here, as already reported (Dowdeswell *et al.*, 1957), there is a population of *M. jurtina* whose females are unimodal at 0 spots. Although its habitat is connected at low tide by a rocky bar with White Island, there is no doubt that this population in Top Rock Valley is completely isolated from it. From 1953 when it was first sampled, it has maintained a strong heterogeneity against the population of the Main Area of St Martin's, from which it is isolated by a wide band of bare, podsolised soil and by further stretches of poor land covered with bracken. In this region very few specimens of *M. jurtina* have been seen, though it is possible that some slight leakage occurs, as may also be the case in the parallel situation on Tresco (p. 346).

We planned to estimate the size of the population in Top Rock Valley and to plant in it as many females as possible from White Island. It may be assumed that virtually all flying females have already been inseminated. If transferred to another habitat their progeny will therefore carry the genotypes of the original population. After a few generations in which the native population of Top Rock Valley has been flooded with White Island specimens it is hoped to obtain further evidence on the problem posed by the similar adjustments of the two isolated communities. If it is found that the recipient one does not change, then this would suggest either that the White Island genotypes were not mingling with those of the Top Rock Valley population, or that the adjustment to the similar micro-ecological situations in the two habitats has been achieved in substantially similar ways in both. (The second of these alternatives is inherently more probable than the first.) If, on the other hand, we found some disturbance taking place in Top Rock Valley, and if this were not attributable to an alteration in the local micro-ecology, then we would be inclined to think that the similar spot-distributions had arisen by chance from two separate types of genetic adjustment.

This plan has been somewhat disturbed by two adverse events in 1957, but we have pursued it so far as possible and intend to continue with it, so long as it is feasible. Firstly, the drought and warmth of the first half of 1957 had a strong influence on the micro-ecology of

Top Rock Valley. As in so many other habitats in Scilly, the grass became very poor, bracken was sparse and the bramble was strikingly reduced; fæcal traces of rabbits were abundant. Bleached stems over 3 yards long could be seen around some of the bramble clumps indicating the luxuriance of the fruiting growth of 1956. The 1957 growth was wretchedly poor, sometimes hardly exceeding a foot in length. Very much better growth in 1958 was promised, in that the new shoots were a reasonable length, though they were not so strong as the skeletal remains of 1956. This cycle of events is important because bramble, especially in exposed places like Top Rock Valley, provides the shelter for what long grass there is. The soil inland from Top Rock Valley and from the coastal area to the west of it, called Pernagie (sub-area "J" in fig. 3), failed to support the usual luxuriant growth of bracken, which we found to be very short and relatively sparse. This may result in a temporary increase in leakage from the Main Area population on the crown of the island down to the normally isolated north-west coast.

Our second difficulty in carrying out our plan arose from short-term climatic factors. After estimating the population of Top Rock Valley, we returned to White Island to collect live females, but were confronted with high wind which persisted over three days—an unusual event in August on the Isles of Scilly. From what we knew to be a reasonably abundant population, we were able to catch only 14 females which were liberated in Top Rock Valley.

Our estimate of the population of Top Rock Valley was carried out according to the method of Dowdeswell, Fisher and Ford (1949). A daily survival ratio of 84 per cent. reduced the gap between observed and expected survival to minimal proportions, and the resultant population estimates were 169 on 19th August (in perfect collecting weather), 51 on 21st August and 90 on 24th August. The two latter days were less favourable. Allowing for sampling errors in an experiment which had to be carried out on rather a small scale, we might suggest a daily flying population of the order of 100 and a total emergence not greatly exceeding 1000. It is interesting to note that an 84 per cent. daily survival ratio falls between the 89 per cent. calculated by Dowdeswell *et al.* (1949) for the large populations of Tean Areas 1 and 3 and the 75 per cent. calculated for the small population on the very restricted Tean Area 5. Between 1941 and 1945 the calculated daily survival ratio of *Panaxia dominula* at Cothill was 84 per cent. (Fisher and Ford, 1947).

The female spot-distribution found in Top Rock Valley is recorded in table 13 and conforms fairly closely to the distribution found in the period 1953-55. It is, however, becoming apparent that, though the percentages at 0 spots, 1 spot and 2 spots remain similar both from year to year and between Top Rock Valley and White Island, there is a marked and significant tendency for the "tail"—that is female specimens at 3, 4 and 5 spots—to be well represented in Top Rock

Valley while it is virtually absent from White Island. Thus a comparison of the summed distributions for Top Rock Valley and for White Island (1953-57) yields $\chi^2_{(2)} = 2{\cdot}34$; $0{\cdot}5 > P > 0{\cdot}3$, when the "tail" is grouped with the 2-spot category, but $\chi^2_{(3)} = 14{\cdot}88$; $0{\cdot}01 > P > 0{\cdot}001$, when the "tail" is computed separately.

Without the abundant records which we are now accumulating, this difference would be overlooked. It remains firmly established, of course, that the most important adjustments occur in the 0 spot or 2 spot levels of the females throughout Scilly. The difference in "tail" is an example of a "second-order" variation, and should be compared with the "second-order" distinction between the Main Areas of St Mary's on the one hand and of St Martin's and Tresco on the other (see pp. 333-4), or with the small but significant differences between the males of the eastern and western parts of Southern England (McWhirter, 1957). We are inclined to attribute the high "tail" of the Top Rock Valley population to the influence of leakage from the Main Area of St Martin's where the 3-spot condition is well represented. This view receives a little support from the male distribution recorded for the first time in Top Rock Valley in 1957. Table 13 shows that the spot-average for a small sample of males caught there was 2·25, which is rather high. This small sample may possibly include some Main Area males which have come through the much weakened barrier of bracken. As we have seen in the Farm Area on Tresco, however, the selective forces in peculiar and isolated regions such as Top Rock Valley are quite strong enough to maintain a special genetic structure against pressure from another population.

The phenotypes of the fourteen females released in Top Rock Valley on 24th August were: 7 at 0 spots, 4 at 1 spot and 3 at 2 spots.

(iii) *Pernagie*

This is a region of large fields of quite a different character from the usual bulb fields on St Martin's. It lies along the north-west coast of the island from Pernagie Point in the south up to the promontory facing Plumb Island 400 yards to the north. It is marked as sub-area "J" in fig. 3. At the present time these large flat fields are not intensively grazed and in the southern portion of the area around Pernagie Point there is much rank grass and undiminished bracken and bramble, somewhat reminiscent of the current condition of Tean Area 3, and not apparently highly favoured by *M. jurtina*.

We had not until 1957 sampled the Pernagie region, but had collected Top Rock Valley up to the western boundary marked in fig. 3, beyond which the butterfly appeared to be rare. In view of the current plan of assessing the population of Top Rock Valley, however, it seemed to us to be of some importance to explore Pernagie (sub-area "J") more thoroughly. First, there is no real boundary between the two sub-areas. On the other hand, we never found any of the insects

marked in Top Rock Valley in the Pernagie region. This may simply have been due to the prevailing westerly winds at that time. Secondly, as table 13 indicates, we found that the female population of Pernagie is similar to that of Top Rock Valley in having a marked mode at 0 spots. The number of specimens at 1 spot was somewhat lower in Pernagie but these differences are well within the limit of sampling error ($\chi^2_{(1)} = 0{\cdot}22$; $0{\cdot}7 > P > 0{\cdot}5$), and we felt justified in provisionally regarding the Pernagie population as an extension of that of Top Rock Valley and as being isolated in the same way from the populations of the Main Area of St Martin's.

To the south of Pernagie along the coast of Porth Seal, the strip of grazing land narrows until the dense bracken characteristic of the northern slopes of the island comes down to the sea and cuts off the

TABLE 13

Spot-distribution of male and female M. jurtina *in two isolated parts of St Martin's*

	Male spots						Female spots					
	0	1	2	3	4	Total	0	1	2	3	4	Total
Top Rock Valley (sub-area "K")	...	1	14	4	1	20	33	19	6	1	...	59
Pernagie (sub-area "J")	...	...	...	...	1	1	13	2	2	3	1	21
Total . .	...	1	14	4	2	21	46	21	8	4	1	80

Pernagie region from Tinkler's Hill (marked in fig. 3 as sub-area " H "), and from sub-area " B " which lies a few hundred yards farther to the west. It seems likely that the isolation of the Pernagie popu lation on this flank is virtually complete, though, as in the case of Top Rock Valley, we suspect there may be some leakage from the Main Area along the footpaths leading into the fields from the east.

3. SMALL ISLANDS

(1) *Tean*

In a previous paper (Dowdeswell *et al.*, 1957), we have summarised the results of our work on Tean during 1954 and 1955. This revealed certain important changes in the ecology of the island following the removal of a herd of cattle in the late summer of 1950. Vegetation which was previously close-cropped had by 1952 grown rank, so that areas which formerly acted as barriers to *M. jurtina* had become colonised by it, and the reverse. The rapid spread of bracken had enabled the population in area 1 to spread into area 2 (see map,

Dowdeswell *et al.*, 1957), while retaining the spot-distribution characteristic of area 1 since 1946. Area 3, where the insect was previously abundant, was now greatly overgrown with bramble and bracken and had become an effective barrier to it. The small colony of *jurtina* formerly isolated in area 5 had spread into area 4, which had previously barred its way when the grass had been grazed too closely to provide it with shelter or suitable food. Unlike areas 1 and 2 which are rather similar, the ecological conditions in areas 4 and 5 are very different from one another. It was not surprising, therefore, to find that the spotting of the butterflies inhabiting them differed both from that in area 1 (now areas 1 and 2) and from the type found in area 5 at the time when area 4 was still a barrier.

On visiting Tean in 1956, we found conditions much the same as in the preceding year. The only noticeable difference was a great increase in the rabbit population whose grazing had had the effect of

TABLE 14

Spot-distribution in male M. jurtina *on Tean (area 1) in 1954 and 1956*

Spots	0	1	2	3	4	5	Total	Difference
1954 . .	2	16	90	26	9	2	145	$\chi^2_{(3)} = 7{\cdot}59$,
1956 . .	2	8	62	38	9	2	121	$0{\cdot}10 > P \geqq 0{\cdot}05$

reducing considerably the length of grass in area 4, and to a lesser extent in area 2. Although not a barrier in 1954, area 4 had become partially so in 1956. However, observation showed that a small passage of *jurtina* was still taking place along this western limb of the island.

(*a*) *Males*. Previous work on Tean had established that a stable form of spotting (unimodal at 2 spots) had existed throughout the island since our investigations began in 1946. In 1954 only one male sample was collected (from area 1), and this is compared with its 1956 counterpart in table 14.

This shows that there had been a tendency towards increased spotting which, however, has not become fully significant during this period: a tendency which appears to have been universal both on the Mainland and in Scilly during these years.

Samples obtained during 1956 in areas 1, 2, 4 and 5 are compared in table 15.

From a $2 \times n$ table it is clear that spotting was homogeneous in all four areas (as far as the small numbers in area 5 permit any opinion to be formed in regard to that habitat), as previous experience would lead us to expect.

(*b*) *Females.* Extensive sampling of the female *jurtina* population on Tean was last carried out in 1954, and a small collection made from area 1 in 1955 suggested strongly that no appreciable change had taken place since the previous year. It was therefore of some importance, in view of the rapid alterations in the ecology of the island, to obtain

TABLE 15

Spot-distribution in male M. jurtina *on Tean (areas 1, 2, 4 and 5) in 1956*

Spots	0	1	2	3	4	5	Total	Difference
Area 1 . .	2	8	62	38	9	2	121	$\chi^2_{(3)} = 0{\cdot}84$,
Area 2 . .	5	9	60	40	4	1	119	$0{\cdot}9 > P > 0{\cdot}8$
Area 4 . .	...	2	23	13	4	...	42	
Area 5 . .	...	1	11	11	...	...	23	

samples in 1956 for comparison with those of two years before. These comparisons are made in table 16.

The poor samples from areas 4 and 5 in 1956 were due entirely to the scarcity of *jurtina* in spite of good collecting conditions.

TABLE 16

Comparison of spot-distribution in female M. jurtina *from four areas of Tean in 1954 and 1956*

Spots	0	1	2	3	4	5	Total	Difference
Area 1, 1954 .	30	14	49	11	1	1	106	$\chi^2_{(3)} = 0{\cdot}201$,
1956 .	43	22	67	15	5	...	152	$0{\cdot}98 > P > 0{\cdot}95$
Area 2* 1954 .	31	19	55	3	...	...	108	$\chi^2_{(3)} = 6{\cdot}537$,
1956 .	29	31	64	8	4	1	137	$P > 0{\cdot}1$
Area 4, 1954 .	13	17	62	8	6	3	109	$\chi^2_{(3)} = 2{\cdot}013$,
1956 .	9	6	22	7	1	...	45	$0{\cdot}7 > P > 0{\cdot}5$
Area 5, 1954 .	13	18	68	11	5	...	115	$\chi^2_{(3)} = 5{\cdot}335$,
1956 .	9	7	15	5	1	...	37	$0{\cdot}2 > P > 0{\cdot}1$

* North edge.

From the values of χ^2 it is clear that none of the populations has altered significantly during the two years in question. The extremely close accord in area 1 is of much interest since it is precisely what might be expected in this habitat: the only one of the four which has never been subject to change. Thus a comparison of the female samples for the four areas on Tean in 1956 (table 16) confirms our 1954 findings in respect of area 3 which still remained a barrier to *M. jurtina*, separating the populations to the south and west. It does so too in area 1,

which has never so far changed since the observations began in 1946 and for area 2 which represents an extension of area 1 and again proved similar to it ($\chi^2_{(3)} = 5{\cdot}04$; $0{\cdot}2 > P > 0{\cdot}1$). It will be noticed, however, that the populations in areas 4+5 have begun to show a second, though slight, mode at 0 again, having been unimodal at 2 spots in 1954. That is to say, they are reverting to the form normal on Tean, probably because rabbit grazing was restoring the grass on the newly colonised area 4 to the conditions which had previously existed there when grazed by cattle. Consequently areas 1+2 and 4+5 are no longer significantly distinct in 1956 ($\chi^2_{(3)} = 2{\cdot}07$; $0{\cdot}7 > P > 0{\cdot}5$), as they were in 1954.

(ii) *Great Ganilly*

Males were collected on Great Ganilly in 1951, 1955, 1956 and 1957, but not in 1953 (see tables 17 and 18). The combined samples over these four years are together highly heterogeneous ($\chi^2_{(6)} = 30{\cdot}607$, with $P < 0{\cdot}001$). Inspection suggests that this is due to a change which occurred between 1955 and 1956. In the two years prior to 1956 the samples were, as expected, unimodal at two spots. In 1956 and 1957 we encountered the entirely exceptional condition of male samples with a mode at more than two. The 1951 and 1955 distributions prove, in fact, to be homogeneous ($\chi^2_{(2)} = 2{\cdot}80$, $P > 0{\cdot}2$). Owing to the exceptionally hot, dry summer which brought out the species unusually early, the male sample in 1957 is too small to provide a detailed comparison with that of the previous year, though fig. 1 suggests that there has been a steady increase in male spotting between 1955 and 1957: a trend which was found also in most other islands. The higher spot value of the small 1957 sample is not formally significant (for the comparison, $\chi^2_{(2)} = 3{\cdot}81$, with P just under $0{\cdot}2$), but it is evident that its true mode must be either at 3 or 4 spots, not at 2 as in 1951 and 1955.

An inspection of the 5 female samples from 1951 to 1957 (table 18) suggests a distinct change in the spotting of that sex between 1951 and 1953. All are bimodal at 0 and 2 spots, but in 1951 the greater mode is at 0, while subsequently and consistently it is at 2. Indeed the 4 samples from 1953 to 1957 inclusive are homogeneous ($\chi^2_{(9)} = 8{\cdot}27$, with $P = 0{\cdot}5$ approximately). The disparity of the 1951 captures is not quite sufficient to produce total heterogeneity when compared with the other four years in a table of general contingency ($\chi^2_{(12)} = 17{\cdot}48$, with P between $0{\cdot}1$ and $0{\cdot}2$). When, however, the 4 samples from 1953 to 1957 are combined, which their homogeneity fully allows, and then compared with the one from 1951 in a $2 \times n$ table, the distinction of the latter is established, for then $\chi^2_{(3)} = 9{\cdot}05$, with P between $0{\cdot}05$ and $0{\cdot}02$.

It appears, therefore, that some change has affected the *Maniola jurtina* population of Great Ganilly; one which influenced the females before the males and tended still further to increase the spot-averages

of both sexes. This was perhaps of an ecological kind, but its nature is not clear. When, on studying our results up to 1955 (Dowdeswell *et al.*, 1957), we first had some indication of such an adjustment, our comment was: " The vegetation of Great Ganilly differs somewhat from that of any small island we have studied so far, consisting of a

TABLE 17

Great Ganilly—males

Spots	1951	1955	1956	1957	Total
0	...	...	1	...	1
1	2	1	1	...	4
2	33	20	31	3	87
3	27	10	48	8	93
4	13	1	38	9	61
5	1	2	5	4	12
Total	76	34	124	24	258

No male sample was taken in 1953.

luxuriant growth of various grasses. There is, in addition, much heather interspersed with short grass, which is to be found mainly on the higher ground. It may be that in these abnormal circumstances the insect is particularly sensitive to small environmental changes."

TABLE 18

Great Ganilly—females

Spots	1951	1953	1955	1956	1957	Total
0	41	32	13	27	20	133
1	7	13	9	17	10	56
2	37	52	33	35	27	184
3	8	6	6	10	7	37
4	5	2	1	2	3	13
5	...	...	...	2*	...	2
Total	98	105	62	93	67	425

* One of these is actually at 6.

The accumulating information of two further seasons certainly suggests that some change in the habitat, to which the females responded first, has produced a new and perhaps stabilised spot-distribution in the *M. jurtina* population inhabiting it.

(iii) *The Island of Arthur*

We had collected on Arthur, an island of about 25 acres, both in 1951 and 1953. On neither occasion was the population large; though two of us (Dowdeswell and Ford, 1955) were at work for five

or six hours, our totals amounted only to 64 and 77 females respectively. We did not catch males there in either year. The female spot-frequencies proved to be of a highly unusual type, with a very large mode at 2 and a second slight one at 0. The latter was only suggested in 1953, the numbers at 0 and 1 spot being equal. It is an impressive fact that such a distinctive spot-distribution as that encountered in 1951 should be reproduced so closely two years later (for the comparison, $\chi^2_{(3)} = 1{\cdot}99$, for which $P > 0{\cdot}5$).

A visit to the island is not easily combined with other work, and we could not collect there again until 1957. We then found the population reduced to an extremely low level. Two of us (K. G. McW. and E. B. F.) working for about six hours in good conditions, obtained only 9 females and 3 males. Two of these were caught upon Middle Arthur;

TABLE 19

Spot-distributions of a sample from the Island of Arthur, 1957

Spots	Male	Female
0	...	1
1	...	...
(1 or >1)	...	(1)*
2	...	5
(2 or >2)	...	(1)
3	1	1
4	1	...
5	1*	...
	3	9

* These specimens are from Middle Arthur.

this is a small island connected with the main one by a shingle bar about 150 yards long, over which the waves break in rough weather, though it is never actually submerged. The results are shown in table 19. It will be seen that they do not make it possible to estimate the spot-distribution in either sex, except that the large female mode at 2 spots, characteristic of the previous years, is at least suggested this season.

Since the population on Arthur had evidently reached an extremely low density in 1957, it will be important to determine whether the female spot-frequencies there retain their characteristic and unusual form if the numbers should rise again. Should they do so, we shall have a further opportunity to test the theory of "intermittent drift" put forward by Waddington (1957, p. 86) as an explanation of the spot-distributions of this butterfly in Scilly, one which we already have the strongest evidence to disprove (pp. 361-2).

(iv) *White Island*

This small island lies off the north-west coast of St Martin's and is connected with it at low tide. The population of *M. jurtina* on White

Island is undoubtedly isolated by at least 225 yards of rocky terrain from that occupying the shore of St Martin's (see fig. 3). Dowdeswell *et al.* (1957) have described the local situation and a preliminary account of an experiment involving the planting of White Island females on the St Martin's coast is given on pp. 348-50.

We did not collect a sample on White Island in 1956. In 1957 we made two visits and found the collecting area somewhat affected by drought; the population appeared to be smaller than usual, though

TABLE 20

Comparison of female M. jurtina *on White Island in 1957 with samples of 1953-55*

Spots	0	1	2	3	4	5	Total	Spot average	
1953-5	172	90	64	1	...	...	*327*	0·68	$\chi^2_{(2)} = 0{\cdot}074$;
1957	37	18	12	...	...	1	*68*	0·69	$0{\cdot}98 > P > 0{\cdot}95$

there was no approach to the decimation which we found on St Mary's and Tresco. Table 20 presents the results of the catch and it will be readily seen that the females have remained stable with a high mode at 0 spots, as in 1953-55.

In previous years we had not attempted to catch male specimens here in order to save time for other commitments. The maintenance of the high stability of the population into 1957, however, gave us the

TABLE 21

Spot-distribution and spot-average of male M. jurtina *on White Island, 1957*

Spots	0	1	2	3	4	5	Total	Spot-average
1957	1	4	11	2	1	1	*20*	2·05

opportunity of checking whether the correlation of male and female spot-averages, which was a feature of the stable mainland populations in 1950-52 and of at least some of the more highly spotted populations of the Isles of Scilly between 1946 and 1955, could also be found in White Island. Only 20 males were caught in 1957 and their spot-distribution and spot-average are recorded in table 21.

If the two 1957 spot-averages (females 0·69; male 2·05) are entered on a graph (*cf.* McWhirter, 1957) the datum falls among a group of South England populations of the 1950-52 period. Our male sample (although it was rather a small one) appears to be correlated in the same way as in the mainland populations with the female sample.

We now have three bi-sexual samples from low spot-average populations in Scilly, including that from Bryher, 1951, and that from the population on the coast of St Martin's opposite White Island (Top Rock Valley) in 1957, and all three sets of data support this suggestion (fig. 1).

4. DISCUSSION

The de-stabilisation of the large island populations which began in 1956 has fortunately given us an opportunity of studying the process on terrain of which we have an intimate knowledge. It has already enabled us to test certain theories of population dynamics and we may expect that, as the cycle completes itself, further deductions may be drawn concerning the nature and strength of stabilising selection in the field.

It seems clear that the process of de-stabilisation began after the effect of a series of droughts had accumulated to such an extent that the supply and quality of the food-plants of *M. jurtina* were being adversely affected and liability to predation perhaps increased (see p. 339 and pp. 348-50). This had the expected result (McWhirter, 1957) of reducing the relative viability of high-spotted females. Yet the reaction of *M. jurtina* on the three large islands was interestingly different in each case; nil on St Mary's; stepwise and moderate, on St Martin's; violent, on Tresco. This grading of the reaction corresponds with three types of ecological difference. Firstly, the size of the Main Areas of the three islands, that is those areas known to be occupied by populations exhibiting the " flat-top " distribution, varies: St Mary's Main Area is the largest; St Martin's Main Area comes next; Tresco Main Area is the smallest. Secondly, although no quantitative study has yet been attempted, it is probable that the actual sizes of the *M. jurtina* populations are in the same order. St Mary's offers far more acreage suitable to *M. jurtina* than does St Martin's, but the density of the insect on St Mary's is probably rather lower. On Tresco both available acreage and density are much lower than on the other two islands. Thirdly, it happens that the amount of cultivation on St Mary's is greater than that on St Martin's (taken as a whole), while the main area of Tresco is wholly uncultivated. Since conservation of moisture in a sandy soil is one of the main effects of the intensive and efficient agriculture (or horticulture) of Scilly, it is reasonable to suppose that the recent ecological shock was buffered more on St Mary's than elsewhere, and least of all on Tresco. We are strongly inclined to put forward this third comparison as the explanation of the differing reactions; we are dealing with very strong selection pressures which will act as readily on a very large population as on one of moderate size. The slight, presumably genetic, difference between the St Mary's population and the other two, whereby more insects with 3 or more spots are consistently found on St Mary's, may also suggest a greater innate ability to resist the unfavourable effects of drought (p. 336).

An important feature of the present phase of stabilisation in the large islands is that, although there has been a sharp move towards lower spotting in the females, the trend in the males has been in the other direction, towards higher spotting. It is possible that the population on St Mary's is also taking part in this move, even though its females still remain stabilised. Table 22 and fig. 1 illustrate the similarity of response on the three large islands, though it must be emphasised that the 1957 value for St Mary's could only be based on 10 specimens and might be misleading.

A tendency towards higher male spotting seems to have begun in 1956 and continued in 1957. It is quite possible that the ecological

TABLE 22

Comparison of spot-averages of male and female samples of M. jurtina *from the three large islands of Scilly*

Island	Range of spot-averages during period of stabilisation, 1950-55		Spot-averages in 1956		Spot-averages in 1957	
	Males	Females	Males	Females	Males	Females
St Martin's	2·14-2·23	0·99-1·19	2·23	0·95	2·38	0·93
Tresco .	2·12-2·21	1·14-1·24	2·29	1·15	2·60	0·81
St Mary's	2·32	1·12-1·43*	...	...	2·80	1·29

* It should be noted that the range of female spot-averages on St Mary's is not so great as these figures suggest. The low reading (1·12) is from the 1951 sample ; since 1954, when the island was next visited, there has been a steady tendency for the St Mary's females to show a high " tail " of insects with 3, 4 or 5 spots and this has maintained the spot-average between 1·29 and 1·43.

stresses described on pp. 341-2 have opposite effects on the males and on the females or that this increase in male spotting is part of a trend oberved all over Southern England and Cornwall. It is clear, at any rate, that the three populations were stable between 1950 and 1955 and that the male and female spot-averages conformed to the general correlation, oberved not only in Scilly but all over Britain (McWhirter, 1957, fig. 1). When de-stabilisation began in 1956 this correlation between the sexes was broken. Clearly this is a phenomenon comparable with the break-down in correlation observed at the sensitive " boundary " area between Devon and Cornwall (Creed *et al.*, 1959). Until the results of individual breeding tests are available, evidence that spotting is to a large extent heritable must be deduced from population data. Male and female spot-averages are usually strongly correlated in stabilised populations. They tend to deviate from this correlation only in genetically " sensitive " contexts, where

selection-pressures appear to be marginal or in the process of changing. We have here one reason for excluding any extreme environmentalist argument that spotting is a phenotypic phenomenon.

That the " flat-top " stabilisation is governed by a special genetic condition and is not a mere admixture of differently adjusted sub-populations, is proved by the local homogeneity of the St Martin's Main Area samples. We happened to test this for the first time in a year when the population had switched to its characteristic alternative stabilisation; but this was found in three well separated collecting areas (fig. 3).

It seems to be in the nature of stabilised populations that they are insulated against numerous ecological variations (especially, perhaps, those which are frequently experienced); the factors which in Scilly and possibly on the mainland seem to upset stabilisation are in some way linked with the abundance or luxuriance of grass. Stabilisation, however, cannot be regarded as a condition akin to passivity, in which " nothing much " happens to the population, so that it quietly maintains its " ordinary " structure. Such an idea would be utterly contrary to the fundamentals of the theory of natural selection. Stabilisation is the reflection of a dynamic, multi-dimensional, equilibrium. It is scarcely necessary to emphasise that the selective forces maintaining the equilibrium are powerful ones. In *M. jurtina* some hundreds of candidates for parenthood are in an average year reduced to a mere two. While much of this elimination will be random with respect to the particular characters studied, there is ample room for strong selective effects. Indeed rearing experiments by W. H. Dowdeswell show that the genes which control spotting in *M. jurtina* influence the body in other and important ways. When, therefore, in an area of stabilisation, certain of the conflicting forces are strengthened or reduced, and the buffering system supporting the relevant selective factors in the micro-ecological norm collapses, the response of the stabilised organism is likely to be rapid and decisive: in fact, quantised.

Thus we would expect, once we had obtained sufficient background information to establish what is the " normal " equilibrium relating organism and environment, that changes, when they occur, would often be large and sudden rather than small and gradual. Since in practice a micro-ecological buffering system will probably tend to be modifiable in a limited number of directions, the quantum-changes of selective values and of the resultant pressures on the organism will also tend to follow certain definite paths and arrive at new and specific optimal conditions. This would provide the easiest explanation of the " clumping " which can be observed in the spot-distributions of female populations of *M. jurtina*, despite their isolation in various habitats in the Isles of Scilly. Now that the old large-island stabilisation has been, for the time being at least, broken up, we have the opportunity of observing the dynamics of stabilisation both from the

genetical and from the micro-ecological points of view in three populations between which no gene-flow can take place. In *M. jurtina*, the quantum-changes which we have observed locally, inter-seasonally and intra-seasonally, and the system of alternative equilibria, which is now beginning to present a clearer picture, argue powerfully for the concept of stabilisation being maintained by strong selective forces.

Waddington (1957) has put forward an explanation of the variation between the populations of *M. jurtina* in the small islands of Scilly, which he terms " intermittent drift ". Chance survival of certain genotypes when the population is strongly reduced could, according to his view, result in the development of variant populations in isolated habitats as soon as conditions allowed of re-expansion. By observing populations of *M. jurtina* it is possible to test this hypothesis in two ways:

(i) large populations should be found to be stable;
(ii) small populations should *sometimes* be found to have changed on re-expansion.

One might fairly often find a reduced population reconstructing itself as it was before merely by chance unless indeed the spot-distribution concerned was a very uncommon one. Consequently a series of results might be needed before the second test could be applied.

On the other hand, we have ample data which allow us to apply the first test and in every case we are led to reject Waddington's hypothesis. Generally we find that large populations are remarkably stable, but we have now studied five instances in which they have been transformed. The extent of the transformation is usually of the same order as the difference between populations which are adjusted to isolated habitats. The five areas are listed in table 23.

It will be seen from the above that there is no need to invoke any hypothesis of " intermittent drift " to explain the existing observed differences of spot-distributions. Large populations, though usually stable, can from time to time undergo radical and sudden transformations and these can occur without reduction to small numbers. Fluctuations in numbers do, of course, offer exceptional opportunities for evolutionary change (see, for instance, Ford and Ford, 1930, on *Melitæa aurinia*) but even when they occur the bias given to the re-expanding population will be determined by the selective factors in force during the decline and during the early phase of the re-expansion when genetic reorganisation may be taking place. In most of the instances listed above, however, selection has been strong enough to operate on very large populations. The selective disadvantage of 60 per cent. suffered by the high-spotted Tresco females in 1957 is the largest selection-pressure so far calculated in a wild animal in its natural habitat. We have explained elsewhere (Creed *et al.*, 1959) why we do not hesitate to think in these terms. The few instances so far in which the strength of natural selection has been adequately

TABLE 23

Location, years and reference	Initial female spot-distribution	Subsequent female spot-distribution	Size of population	Relevant ecological factors
Southern England, 1955-57 (Creed *et al.*, 1959)	Unimodal (the " Old English " distribution)	" New English " and " Pseudo-Cornish " distributions	Numerous populations of the order of 1000-10,000 insects were affected	Unknown ; probably not connected with the spread of myxomatosis
Boundary Area between Larrick and Tamar River (Cornwall), 1956-57 (Creed *et al.*, 1959)	Shallow mode at 0 spot (the " New English " distribution)	" East Cornish " distribution with major mode at 0, minor mode at 2	At least two populations of more than 1000 insects	Unknown ; the boundary between two stabilisation areas moved 3 miles towards England and both populations in the region were transformed within the year
Tresco, 1956-57 (see pp. 340-4)	" Flat-top " stabilisation	0 and 1 spots equal ; 2 spots reduced to less than half the level of 0 or 1 spot	1956 population was probably of the order of 5000 insects. Heavy reduction in 1957	Cumulative effects of droughts were clearly responsible
St Martin's 1955-57 (see pp. 337-9)	" Flat-top " stabilisation	Gradual move to the St Martin's alternative stabilisation from 1956 ; this has mode at 0, and 1 and 2 spots are equal	Population very large, probably over 10,000 in 1955 and 1956, much reduced in 1957	Cumulative effects of droughts probably responsible
Great Ganilly, 1951-57 (see pp. 354-5)	Bimodal, major mode at 0, minor mode at 2	Bimodal, major mode at 2, minor mode at 0. Very high spot-averages	Population has been very large probably of the order of 10,000 insects every year, except in 1957, when a slight reduction occurred	The ecology is quite different from that of any other island studied ; the reason for the progressive change is not known

tested have combined to demonstrate that it is a far more powerful agent than was generally supposed.

5. SUMMARY

1. Our work upon the evolution of the butterfly *Maniola jurtina* in the Isles of Scilly is here summarised for the years 1956-57.

2. As in the past, we have used a quantitative character, the number of spots on the underside of the hind wings, for analysing the variability of this insect.

3. The " flat-topped " distribution, with approximate equality at 0, 1 and 2 spots, characteristic of the females in the large islands, had previously persisted throughout our work.

4. In 1956 on St Martin's, and in 1957 on Tresco, the stability of the populations broke down to produce a reduction in female, but an increase in male, spotting. However, on St Mary's, the largest and most varied island of the three, the original spotting-type persisted unaltered.

5. The new spot-distributions were correlated with drought which produced an acute shortage of grass, except upon St Mary's.

6. This rapid change in two large populations of *Maniola jurtina* on Scilly in response to exceptional ecological conditions is fatal to Waddington's theory of " intermittent drift ", by which he attempts to explain the uniformity of this insect on the large islands and its difference from one to another of the small islands.

7. By dividing St Martin's into sub-areas, it was shown that the population there is homogeneous, not a mixture of differently adjusted sub-populations.

8. If the uniformity of spotting on the large islands is obtained in response to the average of the conditions there, any small isolated areas upon them may achieve local and differing adjustments. Three such areas have been studied in 1956-57 (one on Tresco and two on St Martin's) and the existence of such local adjustments in them has been proved and analysed.

9. The spot-frequencies of *Maniola jurtina* were studied upon four of the small islands.

10. These frequencies have not changed on White Island; nor have they done so on Tean since the removal of cattle late in 1950 produced a profound difference in the ecology, and consequently in the spotting of *Maniola jurtina*, in certain areas.

11. The butterfly has become very rare on the island of Arthur, while on Great Ganilly an increase in male spotting between 1955 and 1956 has produced the exceptional condition of a mode at 3 spots. An increase in female spotting, to convert the minor mode at 2 spots into a major one, had occurred earlier, between 1951 and 1953.

12. Our results show that the characteristic spot-distributions of the various *Maniola jurtina* populations in Scilly are both maintained

and adjusted by extremely powerful selection-pressures which, in the exceptional conditions of 1957 on Tresco, could be assessed as a 60 per cent. elimination of high-spotted females.

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A BIOMETRICAL ANALYSIS OF MATROCLINOUS INHERITANCE OF GRAIN WEIGHT IN RICE

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1. INTRODUCTION

Cytoplasmic inheritance, as expressed in differences between reciprocal crosses, occurs extensively among cryptograms and angiosperms, and is associated with extreme oögamy. Geneticists no longer consider hereditary transmission the total monopoly of the nucleus, but the mechanism of cytoplasmic inheritance is still imperfectly understood. Systems of self-propagating, extranuclear determinants or plasmagenes have been invoked by various workers (Darlington, 1939; Wright, 1941), but the possibility that, in certain instances, reciprocal differences between crosses result from the persistence in the cytoplasm of delayed nuclear effects must be conceded. The issue can be decided by an exchange of nuclei through repeated backcrossing to the male parent (Michaelis, 1954).

Striking reciprocal differences that derive from disturbances in the normal pattern of development have been the subject of much investigation. The quantitative and less spectacular expressions of matrocliny have received less attention. Quantitative matroclinous differences, however, are probably of greater significance in breeding, and possess the attraction of being more amenable to biometrical analysis. The instance of matroclinous inheritance of grain weight, which forms the subject of the biometrical analysis presented herein, was noted during the course of a study of the genetics of yield components in rice (*Oryza sativa* L.). The authors have been unable to find in the literature on the subject, a previous record of an attempt at the biometrical analysis of a character manifesting matroclinous inheritance.

2. MATERIALS AND METHODS

The rice pure lines *Vellai Ilankalayan 28061* (*v*) and *Panduruwi* (*p*) were used in reciprocal crosses made in 1949, at Peradeniya. Both varieties belong to the *indica* group of *Oryza sativa* L. *Vellai Ilankalayan 28061* possesses the coarse grain that characterises most varieties indigenous to Ceylon. *Panduruwi*, which is finer grained, is a selection within a variety of obscure antecedents, but probably of foreign origin. Progenies derived from these reciprocal crosses were grown in successive generations at the Central Rice Breeding Station, Batalagoda, and the weight of one hundred grains was recorded in hybrid populations and lines. In F_1 plants, the 100-grain weight was calculated from relatively small numbers. Table 1 indicates the numbers of plants and lines investigated in various generations.

3. GRAIN WEIGHT IN PARENTAL AND FILIAL GENERATIONS

Mean values of the 100-grain weight in parental varieties, reciprocal F_1 hybrids and segregating populations are given in table 1.

TABLE 1

100-grain weight in parents F_1, F_2 and F_3

Generation	Notation	Number investigated	100-grain weight (gm.)	
$P_1(p)$	x_0	96 plants	1·78	
$P_2(v)$	y_0	31 ,,	3·02	
$F_1(p \times v)$	x_1	5 ,,	2·02	
$F_1(v \times p)$	y_1	8 ,,	2·47	
$F_2(p \times v)$ No. 25	x_2	74 ,,	2·39	Average : 2·39
$F_2(p \times v)$ No. 31	x_2	15 ,,	2·40	
$F_2(v \times p)$	y_2	184 ,,	2·48	
$F_3(p \times v)$ No. 25	x_3	13 lines	2·36	Average : 2·37
$F_3(p \times v)$ No. 31	x_3	6 ,,	2·38	

The 100-grain weights of the parents were 1·78 gm. and 3·02 gm., with a mid-parental value of 2·40 gm. The differences between reciprocal hybrids in both F_1 and F_2 generations indicate marked matrocliny: the 100-grain weights of $F_1(p \times v)$ and $F_1(v \times p)$ were 2·02 gm. and 2·47 gm. respectively. Reciprocal differences persisted in the F_2 generation: $F_2(v \times p)$ showed a higher value for the 100-grain weight than $F_2(p \times v)$. In the instance of the $p \times v$ cross at least, the maternal effect tended to decline in later generations. It is evident that in the crosses that form the subject of the present investigation, grain weight is controlled not only by nuclear genes but by cytoplasmic factors.

4. THE GENETIC MODEL

The following genetic model which has been constructed to fit the results presented above assumes that the phenotype of the hybrid is determined primarily by its genotype, but is affected by cytoplasmic

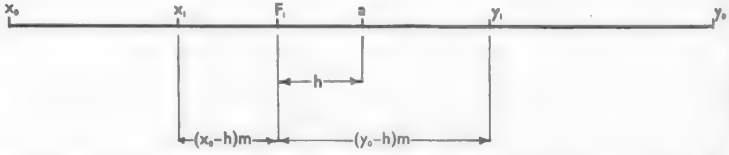

FIG. 1.—Genetic model of grain-weight inheritance in reciprocal hybrids: x_0 and y_0 are the parents, a is the midparental value, h is the deviation due to dominance, and m is a constant that provides a measure of the magnitude of the maternal effect.

factors contributed by the female parent. It is also assumed that the genotype of the female parent influences the nature of these cytoplasmic factors. Fig. 1 gives a diagram of the model.

On the basis of this model, the average phenotypic value of the various hybrid populations will be:

$$\left.\begin{aligned} x_1 &= a+h+\{(x_0-a)-h\}m \\ x_2 &= a+\frac{h}{2}+\left\{(x_1-a)-\frac{h}{2}\right\}m \\ &\vdots \\ x_n &= a+\frac{h}{2^{n-1}}+\left\{(x_{n-1}-a)-\frac{h}{2^{n-1}}\right\}m \end{aligned}\right\} \quad (1)$$

and

$$\left.\begin{aligned} y_1 &= a+h+\{(y_0-a)-h\}m \\ y_2 &= a+\frac{h}{2}+\left\{(y_1-a)-\frac{h}{2}\right\}m \\ &\vdots \\ y_n &= a+\frac{h}{2^{n-1}}+\left\{(y_{n-1}-a)-\frac{h}{2^{n-1}}\right\}m \end{aligned}\right\} \quad (2)$$

x_n and y_n can be re-written in the following form:

$$x_n = a(1-m)+\frac{h}{2^{n-1}}(1-m)+mx_{n-1} \quad (3)$$

and

$$y_n = a(1-m)+\frac{h}{2^{n-1}}(1-m)+my_{n-1} \quad (4)$$

The following two formulæ which are derived from (3) and (4) are functions of parental values:

$$x_n = a(1-m^n)+\frac{h(1-m)}{2^{n-1}}\frac{(1-2^n m^n)}{(1-2m)}+m^n x_0 \quad (5)$$

$$y_n = a(1-m^n)+\frac{h(1-m)}{2^{n-1}}\frac{(1-2^n m^n)}{(1-2m)}+m^n y_0 \quad (6)$$

substituting p for $a(1-m)$ and q for $h(1-m)$, the following equations for securing estimates of a, m and h are obtained.

$$\left.\begin{aligned} x_1 &: p+q+1{\cdot}78m = 2{\cdot}02 \\ y_1 &: p+q+3{\cdot}02m = 2{\cdot}47 \\ x_2 &: p+0{\cdot}5q+2{\cdot}02m = 2{\cdot}39 \\ y_2 &: p+0{\cdot}5q+2{\cdot}47m = 2{\cdot}48 \\ x_3 &: p+0{\cdot}25q+2{\cdot}39m = 2{\cdot}37 \end{aligned}\right\} \quad (7)$$

The least squares method provides the following three simultaneous equations:

$$\left.\begin{aligned} 5p+3{\cdot}25q+11{\cdot}68m &= 11{\cdot}73 \\ 3{\cdot}25p+2{\cdot}5625q+7{\cdot}6425m &= 7{\cdot}5175 \\ 11{\cdot}68p+7{\cdot}6425q+28{\cdot}1822m &= 27{\cdot}6727 \end{aligned}\right\} \quad (8)$$

The c-matrix obtained is

c_{pp} −6·880052	c_{qp} −1·159747	c_{mp} −2·536908
c_{pq} −1·159747	c_{qq} 2·236340	c_{mq} −0·125802
c_{pm} −2·536908	c_{qm} −0·125802	c_{mm} 1·121010

Hence:

$$\left.\begin{aligned} m &= 0{\cdot}3177 \pm 0{\cdot}0710 \\ p &= a(1-m) = 1{\cdot}7815 \pm 0{\cdot}1759 \\ q &= h(1-m) = -0{\cdot}2734 \pm 0{\cdot}1003 \\ \text{and} \quad h &= -0{\cdot}4008 \text{ and } a = 2{\cdot}6111 \end{aligned}\right\} \qquad (9)$$

Table 2 permits the comparison of observed values with expected values for different hybrid populations derived from the above estimates.

TABLE 2

Comparison of observed values with the expected values based on the genetic model

	Observed	Expected
x_1	2·02	2·0736
y_1	2·47	2·4675
x_2	2·39	2·3036
y_2	2·48	2·4288
x_3	2·37	2·4451

Comparison of observed and expected values in different hybrid populations in table 2 using the standard errors of estimated values demonstrates the adequacy of the genetic model.

5. PARTITIONING OF VARIANCE COMPONENTS IN HYBRID POPULATIONS

The methods and notation of Mather (1949) have been used in the partitioning of components of variation in various hybrid populations. The results are presented in table 3.

The observed variance and covariance values in different hybrid populations and the values expected on the basis of estimated D, H and E values described later are presented in table 4.

Equations for deriving estimates of D, H and E are as follows:

$$\left.\begin{aligned} &\mathrm{E}_1 && = 0{\cdot}0072 \\ &\tfrac{1}{2}(1-m)^2\mathrm{D}+\tfrac{1}{4}(1-m)^2\mathrm{H}+\mathrm{E}_1 && = 0{\cdot}0562 \\ &\tfrac{1}{4}(1-m)^2\mathrm{D}+\tfrac{1}{8}(1-m)^2\mathrm{H}+\mathrm{E}_1 && = 0{\cdot}0247 \\ &\tfrac{1}{2}(1-m)^2(1+m)^2\mathrm{D}+\tfrac{1}{16}(1-m)^2(1+2m)^2\mathrm{H}+\mathrm{E}_2 && = 0{\cdot}0415 \\ &\tfrac{1}{8}(1-m)^2\mathrm{D}+\tfrac{1}{16}(1-m)^2\mathrm{H}+\mathrm{E}_1 && = 0{\cdot}0260 \\ &\tfrac{1}{2}(1+m)(1-m)^2\mathrm{D}+\tfrac{1}{8}(1+2m)(1-m)^2\mathrm{H} && = 0{\cdot}0332 \end{aligned}\right\} \qquad (10)$$

Substituting 0·3177 for m (see (9)), and E_2 for $\dfrac{\mathrm{E}_1}{n}$ (where $n = 42{\cdot}20$, the harmonic mean of the number of individuals included in each F_3 line), we derive the following three simultaneous equations by the least squares method:

$$\left.\begin{aligned} 0{\cdot}328532\mathrm{D}+0{\cdot}096196\mathrm{H}+0{\cdot}416921\mathrm{E}_1 &= 0{\cdot}044425 \\ 0{\cdot}096196\mathrm{D}+0{\cdot}032890\mathrm{H}+0{\cdot}205515\mathrm{E}_1 &= 0{\cdot}015124 \\ 0{\cdot}416921\mathrm{D}+0{\cdot}205515\mathrm{H}+4{\cdot}000562\mathrm{E}_1 &= 0{\cdot}115084 \end{aligned}\right\} \qquad (11)$$

TABLE 3

Components of variation in various hybrid populations

	Notation	Components of variation
(1) Variance in parental varieties and reciprocal F_1 hybrids	Vx_0, Vy_0, Vx_1, Vy_1	E_1
(2) Variance in F_2	Vx_2, Vy_2	$\frac{1}{4}(1-m)^2D + \frac{1}{4}(1-m)^2H + E_1$
(3) Within-lines variance in F_2 . .	$Vx_2(Wn)$, $Vy_2(Wn)$	$\frac{1}{4}(1-m)^2D + \frac{1}{8}(1-m)^2H + E_1$
(4) Between-lines variance in F_2 . .	$V\bar{x}_2$, $V\bar{y}_2$	$\frac{1}{4}(1-m)^2(1+m)^2D + \frac{1}{16}(1-m)^2(1+2m)^2H + E_2$
(5) Variance in bulked F_2 . . .	Vx_2, Vy_2	$\frac{1}{4}(1-m)^2(3+4m+2m^2)D + \frac{1}{16}(1-m)^2(3+4m+4m^2)H + E_1$
(6) Within-lines variance in F_4 . .	$Vx_4(Wn)$, $Vy_4(Wn)$	$\frac{1}{8}(1-m)^2D + \frac{1}{16}(1-m)^2H + E_1$
(7) Variance in two backcrosses between F_1 and P	$V_{B(X)}$*$+V_{B(Y)}$*	$\frac{1}{4}(1-m)^2D + \frac{1}{8}(1-m)^2H + 2E_1$
(8) Covariance between F_2 and $\bar{F}_2$.	$Wx_2\bar{x}_2$, $Wy_2\bar{y}_2$	$\frac{1}{4}(1-m)^2(1+m)D + \frac{1}{8}(1-m)^2(1+2m)H$
(9) Covariance between F_2 and $\bar{F}_4$.	Wx_2x_4, Wy_2y_4	$\frac{1}{4}(1+m)(1-m)^2(3+2m+2m^2) + \frac{1}{16}(1-m)^2(3+8m+8m^2)H$

* Backcrosses fall into two groups, X and Y; $V_{B(X)} + V_{B(Y)}$ represents the sum of the variance of an X-group cross and the variance of a Y-group cross. The group X consists of backcrosses of F_1 to x_0; backcrosses to Y_0 compose group Y:

X..... $x_0\times y_1$, $y_1\times x_0$, $x_1\times x_0$, $x_0\times x_1$

Y..... $y_0\times y_1$, $y_1\times y_0$, $x_1\times y_0$, $y_0\times x_1$

TABLE 4

Observed and expected values of variance and covariance in parental varieties and hybrid populations

	Degrees of freedom	V or W	Pooled V or W	Expectation
Parents Vx_0	95	0·0037	0·0072	0·0091
Parents Vy_0	30	0·0159		
F_1 Vx_1	4	0·0041		
F_1 Vy_1	7	0·0192		
F_2 Vx_2 (No. 31)	14	0·0268	0·0562	0·0520
F_2 Vx_2 (No. 25)	73	0·0586		
F_2 Vy_2	183	0·0575		
$F_2(Wn)$ $Vx_2(Wn)$ (No. 25)	915	0·0243	0·0247	0·0305
$F_2(Wn)$ $Vx_2(Wn)$ (No. 31)	790	0·0252		
$F_2(Bn)$ $V\bar{x}_2$ (No. 25)	12	0·0474	0·0415	0·0390
$F_2(Bn)$ $V\bar{x}_2$ (No. 31)	7	0·0314		
$F_4(Wn)$ $Vx_4(Wn)$ (No. 25)	61	0·0375	0·0260	0·0198
$F_4(Wn)$ $Vx_4(Wn)$ (No. 31)	62	0·0147		
F_2/F_2 Wx_2x_2 (No. 25)	12	0·0342	0·0332	0·0398
F_2/F_2 Wx_2x_2 (No. 31)	7	0·0314		

The c-matrix obtained is:

C_{DD} 27·673973	C_{HD} −91·308962	C_{ED} 1·659270
C_{DH} −91·308962	C_{HH} 344·385531	C_{EH} −7·508961
C_{DE} 1·659270	C_{HE} − 7·508961	C_{EE} 0·425044

Estimated values D, H and E_1 are:

$$\left.\begin{aligned} D &= 0{\cdot}0404 \pm 0{\cdot}0392 \\ H &= 0{\cdot}2879 \pm 0{\cdot}1383 \\ E_1 &= 0{\cdot}0091 \pm 0{\cdot}0049 \end{aligned}\right\} \qquad (12)$$

6. HERITABILITY

Components of variation in F_2 populations provide two estimates of heritability. The ratio of genetic variance to total variance measures heritability in the broad sense.

$$\frac{\frac{1}{2}(1-m)^2D+\frac{1}{4}(1-m)^2H}{\frac{1}{2}(1-m)^2D+\frac{1}{4}(1-m)^2H+E_1} = 0{\cdot}7692 \qquad (13)$$

Heritability in the narrow sense is defined as the ratio of additive genetic variance to total variance.

$$\frac{\frac{1}{2}(1-m)^2D}{\frac{1}{2}(1-m)^2D+\frac{1}{4}(1-m)^2H+E_1} = 0{\cdot}4009 \qquad (14)$$

The regression of F_3 lines on F_2 parents furnishes an estimate of heritability intermediate between the above two values.

$$b_{F_3/F_2} = \frac{W_{\bar{F}_3/F_2}}{V_{F_2}} = 0{\cdot}5907 \qquad (15)$$

The correlation coefficient of F_2 individuals and F_3 lines is

$$r_{F_3/F_2} = \frac{W_{\bar{F}_3/F_2}}{\sqrt{V_{F_2} \cdot V_{\bar{F}_3}}} = 0{\cdot}6874 \qquad (16)$$

7. NUMBER OF EFFECTIVE FACTORS

The following calculation of the number of effective factors assumes (*a*) that all the genes have equal additive effects, and (*b*) that one parent carries all the plus allelomorphs and the other parent all the minus allelomorphs.

$$k = \frac{[\frac{1}{2}(\bar{P}_1-\bar{P}_2)]^2}{D} = 9{\cdot}51 \qquad (17)$$

The number of effective factors is estimated to be about ten. It should, of course, be remembered that the assumptions implicit in the formula are unlikely to be completely justified.

8. DISCUSSION

A survey of the voluminous literature on cytoplasmic inheritance is not attempted in the following discussion: for reviews, reference may be made to Caspari (1948) and Michaelis (1954).

The results relating to matroclinous inheritance in the cross reported in this communication fit the hypothesis of extranuclear determinants transmitted to the hybrid through the cytoplasm of the female parent. The effect of these cytoplasm-borne determinants is to shift the phenotypic expression of the progeny towards that of the female parent. The direction of shift suggests that the maternal genotype influences the nature of the determinants.

The agreement between observed and expected values in tables 2 and 4 demonstrates the adequacy of the genetic model proposed in this paper.

The value of m, the coefficient of maternal effect, in grain-weight inheritance in the cross reported herein is 32 per cent. An investigation of matroclinous effects in a wide range of crosses would elucidate the nature of the cytoplasmic determinants involved.

The relation of the matroclinous inheritance of a character to its heritability is of considerable interest. Formulæ (13) and (14) show that the maternal effect depresses heritability. For instance, heritability in the narrow sense is given by the equation:

$$h^2 = \frac{\frac{1}{2}(1-m)^2D}{\frac{1}{2}(1-m)^2D+\frac{1}{4}(1-m)^2H+E_1} = \frac{\frac{1}{2}D}{\frac{1}{2}D+\frac{1}{4}H+E_1/(1-m)^2} \qquad (18)$$

If m assumes a value between 1 and 0 (*i.e.* $1>m>0$), $\frac{E_1}{(1-m)^2}$ becomes larger than E_1, and accordingly the value of h^2 falls.

If the maternal effect is complete, the heritability value will be zero exactly as in a homozygous line. An illustrative example in which D, H and E all assume the value of unity is given in table 5.

TABLE 5

The relation between maternal effect and heritability value

m	Heritability (per cent.)
0	28·6
0·1	25·2
0·2	21·6
0·3	17·9
0·4	14·2
0·5	10·5
0·6	7·1
0·7	4·2
0·8	1·9
0·9	0·5
1·0	0

It is noteworthy that if $E_1 = 0$, *i.e.* if the character under investigation is completely free of environmental variation, the maternal effect would not influence heritability.

The effect of matroclinous inheritance on the mean value of reciprocal-hybrid populations warrants consideration. Table 6 presents a computation of the difference in mean values of grain weight between the two reciprocal-hybrid populations, $(p \times v)$ and $(v \times p)$, over the generations F_1 to F_{10}. It will be noted that with successive selfings, the difference declines rapidly.

TABLE 6

Expected grain weights in reciprocal-hybrid populations

Filial generation	$h \times v$	$v \times h$	Difference
F_1	2·0736	2·4675	0·3939
F_2	2·3036	2·4288	0·1252
F_3	2·4451	2·4848	0·0397
F_4	2·5249	2·5375	0·0126
F_5	2·5674	2·5714	0·0040
F_6	2·5882	2·5896	0·0014
F_7	2·5959	2·5963	0·0004
F_8	2·6034	2·6035	0·0001
F_9	2·60819	2·60823	0·00004
F_{10}	2·60964	2·60966	0·00002

The genetical meaning of the following two formulæ may now be examined:

$$X_n = a(1-m^n)+\frac{h(1-m)}{2^{n-1}}\frac{(1-2^n m^n)}{(1-2m)}+m^n x_0 \qquad (5)$$

and

$$Y_n = a(1-m^n)+\frac{h(1-m)}{2^{n-1}}\frac{(1-2^n m^n)}{(1-2m)}+m^n y_0 \qquad (6)$$

In these two formulæ,

(*a*) if $m = 0$ (*i.e.* there is no maternal effect), then $X_n = Y_n = a+\frac{h}{2^{n-1}}$;

(*b*) if $m = 1$ (*i.e.* the maternal effect is complete), then in any hybrid generation, $X_n = X_0$ and $Y_n = Y_0$;

(*c*) if m assumes a value between 0 and 1 (*i.e.* $1 > m > 0$), the difference between reciprocal hybrid populations attributable to the maternal effect will decrease in successive generations (see table 6).

In the formulæ (5) and (6), if $n \to \infty$, then x_n and y_n approximate a. The difference between reciprocal hybrids is given by the equation,

$$y_n - x_n = m^n(y_0 - x_0) \qquad (19)$$

In this equation, $m^n(y_0-x_0)$ approaches zero if $n \to \infty$, because m has a value between 0 and 1.

9. SUMMARY

1. Grain weight in rice (*Oryza saliva* L.) has been found to exhibit matroclinous inheritance.

2. A genetic model has been constructed on the assumption that a system of extranuclear determinants can (*a*) interact with the genotype, (*b*) be transmitted to the progeny through the female cytoplasm, and (*c*) influence the phenotypic expression of the progeny for one generation.

3. Comparison of the experimental results with expected values computed on the basis of the above-mentioned assumption demonstrates the sufficiency of the hypothetical model.

4. Formulæ relating to grain weight in successive filial generations have been worked out, and components of variation have been partitioned by the methods of Mather (1949).

5. The value of *m*, the coefficient of maternal effect, is 32 per cent.

6. Heritability in the broad sense assumes a value of 0·77; heritability in the narrow sense has a value of 0·40.

7. The number of effective factors approximates ten.

8. The genetical meaning of matroclinous inheritance is discussed.

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THE ORGANISATION OF POLYGENIC ACTIVITY WITHIN A CHROMOSOME IN *DROSOPHILA*

II. VIABILITY

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1. INTRODUCTION

In an earlier paper (Breese and Mather, 1957) we have described an investigation into the distribution, along chromosome III of *Drosophila melanogaster*, of genetic activity affecting the numbers of abdominal and sternopleural chaetae. The starting material comprised chromosomes III from two lines, H and L, selected respectively for high and low numbers of abdominal chaetae. From these were constructed a variety of recombinant chromosomes, each of which included known combinations of segments from the H and L chromosomes III. This was achieved by the use of the so-called " rucuca " marker stock, but as finally produced the recombinant chromosomes themselves contained no marker genes, though they may have contained short segments of material from between the marker genes of the " rucuca " chromosome. The chromosomes built up and the segments of which they were constructed are listed in table 1 and fig. 1 respectively, which are reproduced from the earlier paper. The legends to table and figure provide further information about the recombinant chromosomes, and a full account of the technique of construction is to be found in the earlier paper.

Once constructed, a recombinant chromosome was maintained against *Me Sb* in the male line, and was thus protected from disruption by further recombination and also in large measure from the action of selection. It could, of course, accumulate variation by mutation during its maintenance, and we have evidence that this in fact occurred.

The recombinant chromosomes were tested for their effects chiefly in diallel sets of crosses. The crosses used were always of the types $\frac{\text{I}}{Me\ Sb} \times \frac{\text{J}}{H}$ where I and J indicate any two of the recombinant chromosomes. The *Me Sb* chromosome largely reduces, even if it does not wholly suppress, recombination in the mothers so that the identity of chromosome I is in the main preserved. A cross of this kind yields four types of progeny: $\frac{Me\ Sb}{H}$; $\frac{\text{J}}{Me\ Sb}$; $\frac{\text{I}}{H}$; $\frac{\text{I}}{\text{J}}$. The last class is of course wild type and provides the material for assessing the joint effect

* Now at Welsh Plant Breeding Station, Aberystwyth.

of I and J on the chaeta characters. It will be observed, however, that the first class is constant over all crosses and so may be used as a

TABLE 1

The recombinant wild-type chromosomes constructed and used in the experiments. Capital and small letters indicate segments derived from chromosome III of the H and L lines respectively. The limits of the segments denoted by A-a, B-b, etc. are shown in fig. 1. In Group (c) the constitution in respect of segment D-d is not fully certain as the gene ca *was omitted from the marked chromosome used in the process of construction*

Group	(*a*)	(*b*)	(*c*)	
Parental chromosomes	(1) ABCD = APQRD = AXYZRD (2) abcd = apqrd = axyzrd			
Recombinant chromosomes	(3) aBCD (4) abCD (5) abcD (6) ABCd (7) ABcd (8) Abcd	(9) APqrd (10) APQrd (11) apQRD (12) apqRD	(13) AxyZR(D) (14) AxYZR(D) (15) AXYzR(D) (16) AXyzR(D) (17) AxyzR(D)	(18) axyZr(d) (19) axYZr(d) (20) zXYZr(d) (21) aXYzr(d) (22) aXyzr(d)

basis for comparing the effects of the recombinant chromosomes on the viabilities of their carriers. The crosses which provided the information about chaeta number described in the earlier paper, also yielded

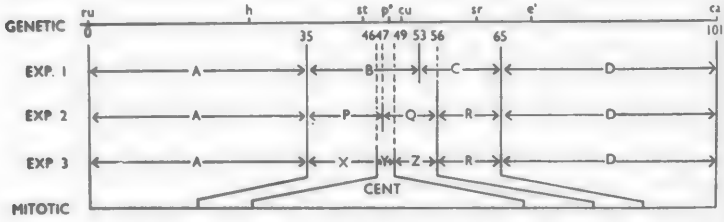

FIG. 1.—The genes used in constructing the wild-type chromosomes and the segments of which, in consequence, these chromosomes were constructed (see in the text).

The extent of each segment is indicated by the arrows, the limits being shown in their average positions. Apart, however, from the left of A and the right of D, the limits might fall by the vagaries of recombination anywhere between the straddling genes (*e.g.* the right limit of A might come anywhere between *h* and *st*) the average position being midway between them on the genetical map. This variation in position of recombination could also lead to a small piece of the marked chromosome being inserted in the region of the limit.

The average positions of all the limits are indicated in relation to the genetical map (above) and some of them also in relation to the mitotic cytological map (below). The general position of the centromere (Cent.) is shown on the mitotic map, though it may well be nearer to the left limit of region Y than is indicated. All positions on this map are very approximate.

From Breese and Mather (1957).

the data on viability now to be described. The various sets of crosses and experiments will be referred to in this paper in the same way as in the earlier report.

2. THE MEASURE OF VIABILITY

In all crosses, the parents were mated for 2-3 days in tubes and then transferred to half-pint milk bottles in which their progeny were raised for counting and recording.

In the first set of crosses made (M1 in the first experiment) the parents remained in the bottles until their early offspring began to emerge. The result was numbers of flies too large for complete classification to be undertaken. Samples of 130-150 were therefore classified from these cultures. In all later crosses, the parents were restricted to 48-60 hours in the bottle, and all the progeny emerging were classified.

At first, in the M1 and M2 sets of crosses in the first experiment, no regard was paid to sex in estimating viability, which was measured as $100\left[\frac{I}{\bar{J}}\right]\Big/\left[\left[\frac{I}{\bar{J}}\right]+\left[\frac{Me\ Sb}{H}\right]\right]$ where $\left[\frac{I}{\bar{J}}\right]$ is the number of wild-type flies of both sexes and $\left[\frac{Me\ Sb}{H}\right]$ the number of flies of both sexes carrying the two marked chromosomes. Equal viabilities of the two classes will then be indicated by a value of 50 per cent. The *H* and *Me Sb* flies were disregarded. These classes could affect the viability as we measured it by affecting the level and outcome of competition among the four classes within the bottle, but any such effect would seem unlikely to be great in the experiments as conducted and its consequences negligible.

A different — and unexpected — complication was, however, revealed by these early sets of crosses. It became clear that the male and female wild-type flies were showing different effects of the recombinant chromosomes III on their viabilities. In all later crosses, therefore, the viability of the wild-type flies was measured separately for males and females. In each case the measure taken was $100\left[\frac{I}{\bar{J}}\right]^{*}\Big/\left[\left[\frac{I}{\bar{J}}\right]^{*}+\left[\frac{Me\ Sb}{H}\right]\right]$ where $\left[\frac{I}{\bar{J}}\right]^{*}$ is the number of wild-type males *or* females, according to which viability was being measured. Males and females were, however, pooled in the $\frac{Me\ Sb}{H}$ class as although there was often a slight shortage of females, in no case was this significant and the ratio borne by the two sexes to one another did not vary significantly over the whole set of experiments. Equal viabilities of the two classes will thus be indicated by a value of $33\frac{1}{3}$ per cent. In every experiment but two where viabilities were measured separately the female proved to vary from cross to cross, as tested by contingency χ^2's measuring the variation in relative numbers of these females and the marked flies (table 2). Further, there was always a significant shortage of the wild-type females when compared with either the wild-type males or the marked flies. As measured by these

χ^2's the viability of males on the other hand failed to show any sign of variation in any experiment, and there was no shortage of these males by comparison with the marked flies. Thus genetic differences in chromosome III are revealed by changes in viability of the females; but these same differences failed to produce comparable changes in the viabilities of the males. Further evidence of this difference between

TABLE 2

Contingency χ^2's testing variation of numbers of wild-type flies relative to Me Sb/H *flies in the various experiments. Males and females were not recorded separately in M1 and M2 of the first experiment so that the test is of variation in the pooled numbers of the two sexes. In all other cases the test is of variation in the numbers of wild-type males and females separately. In all cases the males and females are pooled in the* Me Sb/H *class, as the sex ratio did not vary significantly among these flies*

Experiment	Variation relative to *Me Sb/H* class of numbers of wild-type					
	Females and Males					
	χ^2		N		P (in per cent.)	
1. M1 . .	87·9		48		<0·1	
M2 . .	62·0		48		[illegible]	
	Females			Males		
	χ^2	N	P (in per cent.)	χ^2	N	P (in per cent.)
1. O1 . .	106·4	48	0·1	40·3	48	78
O2 . .	45·1	47	56	35·1	47	90
2. Set 1 . .	80·8	58	3	70·7	58	14
2 . .	71·2	46	1·3	51·7	46	32
3. Set 1 . .	58·3	34	0·6	41·0	34	23
2 . .	38·9	35	35	43·9	35	17
4. . .	55·1	27	0·1	36·7	27	10
Total .	455·8	295	v. small	319·4	295	16

the sexes will be found in the later sections dealing with the individual experiments, though as will be seen it was not so great in the last as in the earlier experiments.

3. THE FIRST EXPERIMENT

In this experiment all the chromosomes (1)-(8) (see table 1), with the exception of (2), were used in a diallel set of crosses, every chromosome being brought from the mother into combination with every chromosome from the father. With 7 chromosomes there were thus 49 combinations including the 7 homozygotes. The 42 heterozygous

combinations fall into 21 pairs, the members of a pair differing only in the way in which the two chromosomes were brought in from the two parents.

The diallel set was made up four times, giving all combinations of two genetic backgrounds (M, the background of the *Me Sb/H* stock, and O, the Oregon background) and the two groups of recombinant chromosomes (1 and 2), these being formally alike but constructed on different occasions so that they may differ as a result of the normal variation in position of crossing-over between the marker genes. One heterozygous combination failed in one of the four replicates. The consequent missing value was replaced by the viability from its reciprocal cross, and the corresponding adjustment made in the degrees of freedom available in the analysis of variance.

In the first two diallel sets (M1 and M2) no distinction was drawn between male and female wild-type flies, but in the O1 and O2 diallel sets of this, and in all later experiments, males and females were counted separated. Pooling males and females in O1 and O2 as well as in M1 and M2, the average viability percentages as defined in section 2 above, were found to be M1-47·4, M2-49·5, O1-46·6 and O2-48·7 in the four diallel sets with a grand average of 48·0, where, of course, 50 per cent. indicates a viability equal to that of the *Me Sb/H* class which was used as the yardstick. When the sexes are taken separately in the O1 and O2 sets 33⅓ per cent. indicates viability equal to that of the *Me Sb/H* class (see section 2) and the average percentages actually found were O1 females 28·8, O2 females 30·6, O1 males 31·9 and O2 males 33·8. Thus overall viabilities are reasonably high: we are not dealing with sub-lethal combinations of genes. The range of viabilities encountered in the females of the O1 and O2 diallel sets is illustrated in fig. 4.

The viability percentages were all transformed into angles (see Fisher and Yates, 1957) before analysis in this and all the other experiments. These viability results were analysed in two ways, as were the chaeta numbers of the earlier paper. This first analysis was by means of the W/V and W/W′ relations of the diallel tables (see Hayman, 1954; Jinks, 1954; and Breese and Mather, 1957). The W/V and W/W′ graphs are shown in fig. 2 for the sexes pooled in the combined M and O replicates, and for the sexes separately in the combined O1 and O2 replicates. The corresponding graph for the abdominal chaetae is also repeated from fig. 2 of the earlier paper for comparison. Each point on the various graphs is numbered to show the recurrent chromosome in the diallel array from which that point is derived. This was also done in fig. 2 of the earlier paper, but unfortunately an incorrect set of numbers was assigned to the points in that figure. The error has been rectified in the present fig. 2, which in this respect therefore corrects and replaces the earlier graph.

Several points emerge from these graphs. In the first place, in contrast to the females, the males of O1 and O2 show little more than

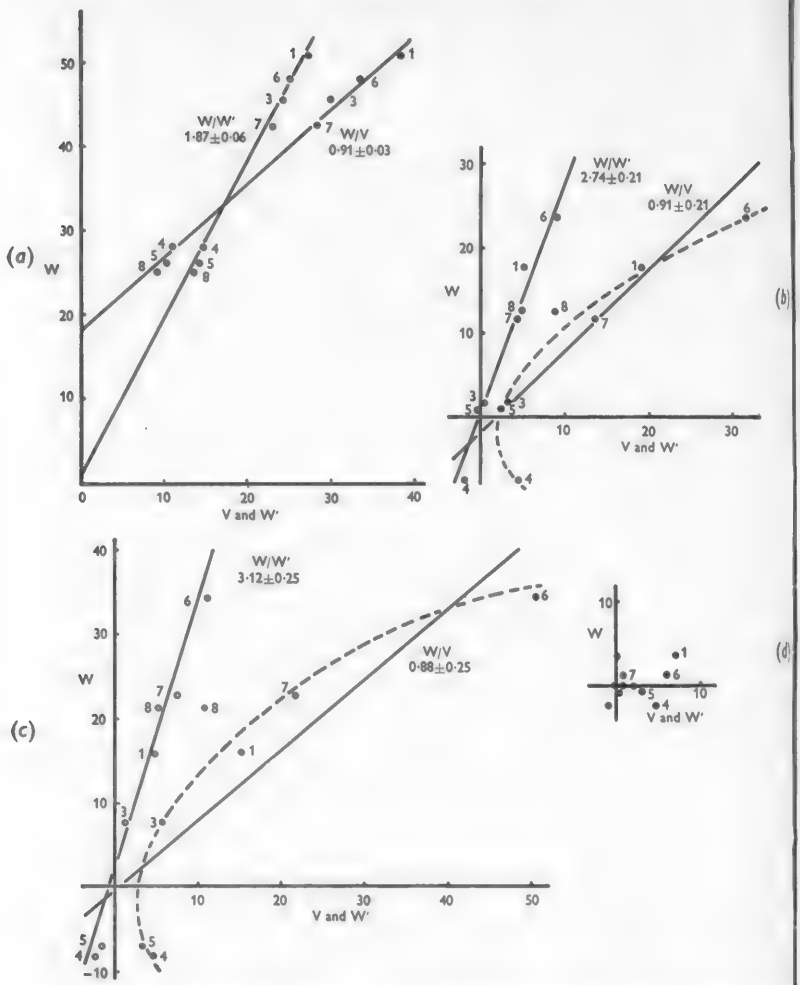

FIG. 2.—The W/V (solid circles) and W/W′ (open circles) graphs from the diallel analyses of the first experiment for (*a*) abdominal chaeta number and (*b*)-(*d*) viability. For (*b*) the data are from the combined sexes in the complete experiment, for (*c*) from females in O1 and O2, and for (*d*) from the corresponding males. The numbers indicate the chromosomes to which the points relate. The straight lines are the best fitting linear regressions, for which the calculated slopes are shown. The dotted curves in (*b*) and (*c*) have no special significance, being included only to bring out the curvilinear nature of the W/V relation in these graphs. For the sake of clarity no regression lines are shown in (*d*), and some of the chromosome numbers are omitted.

Note. (*a*) is from Breese and Mather (1957) where, however, the points were numbered incorrectly in respect of the chromosomes to which they relate. This numbering is now corrected.

random scatter about the point (O, O) in both W/V and W/W′ relations. Completely random scattering round (O, O) would imply a total absence of genetic difference among the seven chromosomes in their effects on viability of the males. The small departure from random scatter shows that this is not fully the case, and indeed we shall see further indications of effects in male viability in other experiments; but the graphs of fig. 2 show that any effect on males is very small as compared with effects on females.

The second point to emerge from the graphs is not only that the females (and, of course, correspondingly the pooled sexes) show striking genetic differences among the seven chromosomes, but also that the genes responsible display both dominance and interaction among themselves. The action of dominance is revealed by the spacing of the array points along the lines in the graphs; and the action of interaction by the curvilinearity of the W/V relation and also by the departure of the W/W′ line from a slope of 2. Slight departures of both kinds were detected in the graphs from chaeta numbers and were ascribed in the earlier paper to causes other than genic interaction. Those in the viability graphs are, however, so much larger and more striking as to leave no doubt that interaction is present and is, to say the least, a much more important feature of the gene system in chromosome III affecting viability than of that affecting chaeta number. We may note, too, that, in so far as the intercept of the best fitting W/V line on the y-axis can still be used to measure dominance where the relation is basically curvilinear, its proximity to the origin indicates complete or virtually complete dominance of the operative combinations of genes for viability as compared with the partial dominance indicated in the case of the chaeta. We shall see further evidence of high dominance later.

The third and last feature to be noted about these graphs is that the seriation of the points relating to the seven individual chromosomes is different in the case of viability from that shown with the chaeta numbers. The place of a point in this seriation reflects the overall dominance, or potence, of the combination of genes carried by the chromosome it represents, the farther down towards the left of the line the greater being the potence. In the case of chaeta number, the main division of the points is between (4), (5) and (8) carrying the more dominant b segment and (1), (3), (6) and (7) carrying the more recessive B segment. The wholly H chromosome, (1), is the most recessive. With viability, however, the B-b segment is no longer outstanding in determining the potence properties and the most recessive and most dominant chromosomes are (6), ABCd, and (4), abCD, respectively. The significance of this observation will be examined in more detail later: the point to note for the moment is that in respect of their contributions to dominance and potence the segments do not behave in the same way for viability as for chaeta number.

The second analysis of the data was by fitting constants to represent

the contribution of the various segments to the additive and dominance variation in viability, just as was done for chaeta number. These constants can be used as the basis for arriving at an analysis of variance which allows the contributions of the different possible sources of variation in viability to be tested for significance (see Breese and Mather, *loc. cit.*). If all four diallel sets are to be brought into a single analysis, the results from the pooled sexes must be used as only these

TABLE 3

Analyses of variance of results of first experiment

Item	N	Mean squares		
		All sets—sexes pooled	O1 and O2	
			Females	Males
Additive effects (A)	4	120·12*	145·50*	9·89
Dominance (D)	4	108·85*	122·26*	33·36†
Res. interaction (I)	19	17·56	28·16*	7·99
Backgrounds (B)	1	10·42	...	...
Groups (G)	1	72·01*	33·39	29·96
B×A, B×D	8	20·79	...	...
B×I	19	9·16	...	...
G×A	4	15·54	2·55	15·89
G×D	4	34·58†	22·00	7·79
G×I	19	13·16	15·21	15·91
Remaining interactions	28	7·13	...	...
Reciprocals	84/41‡	12·77	11·27	8·81
Theoretical error	...	11·47	12·01	11·76

* $P<0.01$.
† $0.05>P>0.01$.
‡ 84 for "All sets" and 41 for the two "O1 and O2" columns. Note that both these values are reduced by 1 owing to a missing cross.
All tests of significance were carried out by means of χ^2's as described in the text.

are available from M1 and M2. For O1 and O2, however, the sexes may be analysed separately. The three analyses of variance, for pooled sexes over all four diallel sets and for the females and males respectively in O1 and O2, are given in table 3 and the average value of the eight constants, a "d" measuring the additive contribution and an "h" measuring the dominance contribution from each segment, are given again for the three different sets of data in table 4.

In contrast with the earlier analyses of chaeta number, no items appear for the sex difference and its interactions in the present analyses. The sexes were not separately recorded in M1 and M2 so that the sex difference cannot be introduced into the analysis of the complete experiment, and where it could be introduced in the analysis of O1 and O2 the position is in fact made clearer by dealing with the sexes quite separately. A slightly different break-down has further been

adopted for a number of items in the present analyses in order to bring out certain special features of the viability results. The tests of significance were also carried out differently. With the chaeta numbers these had to be based on comparisons with error variances estimated from the reciprocal differences and high order interactions. A different possibility is open with the viabilities since these are measured as proportions. When transformed into angles, proportions have a theoretical variance of $\frac{820{\cdot}7}{n}$ (Fisher and Yates, 1957), where n is the total number of individuals from which the proportion is estimated. This number varies, though not too widely, from culture to culture, but a theoretical variance can still be found for use in the analysis by

TABLE 4

The constants measuring the additive and dominance contributions of the four regions in the first experiment. For d a positive value indicates higher viability given by the H segment, and a negative sign higher viability given by the L segment. For h a positive sign indicates dominance in the direction of higher viability

	d_a	d_b	d_c	d_d	h_a	h_b	h_c	h_d	s.e.
All sets—sexes pooled	−0·53	−1·21	−0·48	0·86	1·85*	0·45	0·50	1·38†	0·64
O1 and O2									
Females .	−0·74	−1·39	−0·16	2·04†	2·17†	2·16†	−0·05	2·12†	0·82
Males . .	1·13	−0·89	0·37	0·77	1·62	1·17	−0·08	0·47	

* $P<0{\cdot}01$. † $0{\cdot}05>P>0{\cdot}01$.

taking the harmonic mean of the different numbers of individuals counted in the various crosses and using this as the value for n in the formula. The error variances so obtained are given in the bottom line of table 3. Where such a theoretical variance is available, the ratio borne by any sum of squares in the analysis to the theoretical error is distributed as a χ^2 for the number of degrees of freedom appropriate to the sum of squares. All the tests of significance of table 3 have been carried out in this way.

It is encouraging to see in table 3 that the differences between reciprocal crosses and the high order interactions nowhere significantly exceed the theoretical sampling variation and indeed in most cases are slightly, though again not significantly, sub-normal. Evidently there is no unexpected or unaccounted major source of variation in the experiments. Taking first the analysis of the complete experiment, there is no doubt of the genetic effect of chromosome III on viability in respect of both additive and dominance components. The effect of residual non-allelic interactions among the segments is not fully significant. The probability for this item is, however, very little above 5 per cent. ($\chi^2_{[19]} = 29{\cdot}09$ as compared with $\chi^2_{[19]} = 30{\cdot}14$ at $P = 0{\cdot}05$)

and taking this in conjunction with the graphs of fig. 2, there can be little doubt that interactions are having their effects. The difference between backgrounds (M *versus* O) appears to be without importance but the differences between the formally similar recombinant chromosomes of the two groups, 1 and 2, are significant. Evidently the precise positions of the points of recombination are important in respect of viability. Furthermore there is an indication that the effect on dominance varies differently with groups, though that of the additive components does not.

The female viabilities in sets O1 and O2 can obviously give no information about the effects of background or its interactions. In other respects, however, these females not only test the same effects but confirm the complete analysis in a remarkable way. The residual genetic interactions now emerge as fully significant, and while the effects of groups and the G × D interaction are sub-significant their mean squares are both large and, again in conformity with the full analysis, that for G × A is small.

The male viabilities are in striking contrast. No item is significant except for the dominance effects and that has a probability higher than 2 per cent. With eight items tested it would not be unduly surprising to find one of them showing by chance a probability of just below 5 per cent. Thus no great weight can be placed on this single significant item. Indeed if we sum the χ^2's for all eight items in this male analysis we find $\chi^2_{[96]} = 94{\cdot}04$ with a probability of 0·48. The sex difference in the expression of the genetic effects of chromosome III on viability in this experiment is clear from the analysis of variance which completely confirms the conclusion reached from the diallel graphs of fig. 2, *c* and *d*.

One further point remains to be noted about the genetic interactions among the segments as shown by the analysis of females. This gives a mean square of 28·16 as compared with 145·50 for additive effects—a ratio of $\frac{1}{5{\cdot}17}$ or $\frac{1}{8{\cdot}27}$ if both mean squares are reduced by the theoretical error variance. This compares with corresponding ratios of $\frac{1}{225}$ and $\frac{1}{310}$ for abdominal chaeta. Relative to additive effects interactions loom larger in respect of their contribution to the variation in viability than they do in respect of variability in chaeta number, as indeed does dominance also.

The importance of dominance emerges also from the eight constants, the four d's and four h's attributable to the four segments, shown in table 4. Here again the males of O1 and O2 show no significant genetic effects. Tested against their empirical standard error, by no means all of the constants are individually significant in the O1 and O2 females or the pooled sexes of all four diallel sets. There can be little doubt of the additive effect exerted by segment D-d (constant d_d)

and it will be observed that in both sets of results this is of sign opposite to d_a, d_b and d_c. The D segment from the H line evidently makes for higher viability than does its counterpart from the L line, whereas in all the other three segments the L line appears to make for a higher viability than does the H. Significant dominance is indicated by h_a, h_b and h_d in three of the four segments, it being in every case in the direction of dominance for higher viability. Furthermore the h's are on the whole higher in value than the d's suggesting what, for want of a better term, might be described as " over-dominance " in these three segments; though we must note that even where demonstrated such " over-dominance " of a segment carries no implication of over-dominance at any single gene locus in the chromosome.

These findings about the distribution of the additive effects between H and L chromosomes and about dominance again agree, at least broadly, with the conclusions to be drawn from the diallel graphs in fig. 2 *b* and *c*. The chromosome ABCd (No. 6) is farthest up to the right in both diallel graphs, showing that it is the most recessive of the seven. This is to be expected since dominance is for high viability and the A, B and C segments from the H line and the d segment from the L line all give lower viabilities than do their counterparts. Similarly the chromosome abcD (No. 5) is at the other end of the line as would be expected. It is more difficult to sort out the effects of the individual segments from the remaining points in the figure as the structure of the diallel sets is not orthogonal in respect of the segments, but so far as can be judged they are in full agreement with the expectations from table 4.

4. THE REMAINING EXPERIMENTS

The remaining three experiments undertaken for the analysis of the control of chaeta number are less informative than the first one about viability. The fourth experiment is of a different type and as we shall see yields somewhat disparate results. The second experiment ran into such difficulties from missing cultures that its full analysis was impossible even in respect of chaeta number, while both it and the third experiment were undertaken to analyse further the B-b segment which had proved to be of prime importance in the mediation of chaeta number but is of less dominating significance for viability.

(i) The chromosomes used in the second experiment were (3), (5), (6), (8), (9), (10), (11) and (12) of table 1. They confound the effects of segments A-a and D-d, A always being present with d and a with D. At the same time they break segments B-b and C-c down into three new segments P-p, Q-q and R-r (fig. 1). The diallel set of crosses among the eight chromosomes was attempted twice, different groups of recombinant chromosomes being used on the two occasions. As we have noted, so many combinations failed as to make diallel analysis impossible. A partial analysis of variance was, however, attempted from each set of crosses, by fitting constants. The results

are shown in table 5, which sets out the analyses of variance, and table 6, which sets out the constants themselves and compares these with the corresponding groups of constants obtained from the first

TABLE 5

Analyses of variance of results of second experiment. The entries under "Females" and "Males" in the body of the table are mean squares

Item	1st diallel			2nd diallel		
	N	Females	Males	N	Females	Males
Components . .	8	43·8*	15·2	8	38·4*	17·9
Res. Interaction .	26	12·3	9·7	18	18·4	16·8
Reciprocals . .	24	8·3	19·1*	20	11·3	13·9
Theoretical error .	...	10·7	10·7	...	12·2	11·9

* $P<0.01$. † $0.05>P>0.01$.

experiment. The d and h components were not fitted separately in these analyses, so that in table 5 the item for components covers both additive and dominance effects.

TABLE 6

A. *Additive and dominance components of variation in the second experiment. The figures given are averages over the two diallels*

	d_{a-d}	d_p	d_q	d_r	h_{a+d}	h_p	h_q	h_r	s.e.
Females .	−0·95	0·02	−2·23†	0·66	2·32†	−0·12	0·61	0·16	0·84
Males .	0·23	0·72	−0·04	−0·74	1·32	0·31	0·28	−1·37	

† $0.01<P<0.05$.

B. *Comparison of components from first and second experiments*

	d_{a-d}	h_{a+d}	d_b+d_c*	h_b+h_c
Females				
1st experiment .	−2·78	4·29	−1·55	2·10
2nd experiment .	0·95	2·32	1·55	0·65
Males				
1st experiment .	0·37	2·10	−0·52	1·09
2nd experiment .	0·23	1·32	−0·06	−0·78

* Regions B+C in first experiment = P+Q+R in second experiment.

Results are presented separately for males and females in both tables. The analyses of variance for the males reveal no item significant against the theoretical error variance except that for reciprocal

differences in the first diallel. This could easily be due to the vagaries of sampling, and indeed if we take all four "reciprocals" mean squares together there is little to suggest anything beyond sampling variation. The main effects for components are significant in females in both diallels. In this they differ from the males just as in the first experiment. No good evidence of residual interaction appears from either set of crosses.

Again in conformity with the first experiment, the only significant constants in table 6A are from the females, though the high standard errors (denoted s.e. in the table) render their individual values rather uninformative. The components are compared for the two experiments in table 6B, where the summed actions of regions B and C are set against those of P, Q and R to which they correspond when taken together.

TABLE 7

Analysis of variance of third experiment. The entries in the main body of the table are mean squares

Item	N	Females	Males
Components (C) . .	[illegible]	85·2*	13·2
Res. interactions (I) . .	14	15·2	37·6*
Diallels (D) . . .	1	26·6	90·0*
D×C	6	49·3*	25·8
D×I	14	14·3	18·4
Reciprocals . . .	29	11·9	19·1
Theoretical error . .	...	16·2	15·8

* $P<0{\cdot}01$.

Again agreement is as good as could be expected in view of the large standard errors attaching to all entries in the table.

(ii) The third experiment consisted of two diallels, one including chromosomes (1) and (13)-(17) and the other chromosomes (2) and (18)-(20) of table 1. Both of them provide information about the effects of regions X-x, Y-y and Z-z into which regions P-p and Q-q have been jointly broken down (see fig. 1). The two diallels differ, however, in the ways they incorporate the effects of regions A-a, D-d and R-r, so that their overall contrast with one another cannot be interpreted unambiguously. Two combinations (one for each sex) which failed to yield results in this experiment have been given the value of their reciprocals. The numbers of degrees of freedom (N) have been correspondingly adjusted. Four other cultures also failed but were replaced by corresponding cultures raised on a later occasion. The analysis of variance and values of the components are shown for the sexes separately in tables 7 and 8.

The analysis of variance shows the contributions of the three regions, X, Y and Z, to be significant in females and their effects would appear to vary between the two diallels. There is no significant

evidence of interaction in this sex. Curiously enough, however, the item for interaction is significant in the males as is also that for the difference between the diallels. The interpretation of especially the former item is not, however, obvious in the absence of any significant effect of components.

No single component is significant in table 8A. This is not surprising in view of the large standard error attaching to the estimates and in view of the restricted range of the segments under examination as compared with those of the first experiment. Nevertheless, so far as they go, the components of variation set out in table 6A agree with

TABLE 8

A. *Additive and dominance components of variation in the third experiment. The figures given are averages over the two diallels*

	d_x	d_y	d_z	h_x	h_y	h_z	s.e.
Females .	−2·34	−1·56	−1·04	1·15	1·99	0·77	1·56
Males .	0·41	0·06	0·58	−0·05	1·50	−1·15	

B. *Comparison of components from second and third experiments*

	d_{p+q}	h_{p+q}	d_{x+y+z}	h_{x+y+z}
Females . .	−2·21	0·49	−4·94	3·91
Males . . .	0·68	0·59	−0·11	−0·15

Regions P+Q in 2nd experiment = X+Y+Z in 3rd experiment.

expectation. The female components are in general larger and more consistent that the male. Thus all the female d components are negative and all the h's positive. Furthermore the results from this third experiment agree as well as might be expected with those from the second experiment (table 8B).

(iii) The fourth experiment was of a different kind from the second and third. Eight homozygotes were raised and compared, the eight comprising every combination of the compound regions A-a, PQ-pq and RD-rd. The experiment was carried out in quadruplicate but a few cultures failed in some replicates, none, however, failing in all replicates. This is reflected in the degrees of freedom for variation between like cultures being fewer than the basis design of the experiment would lead one to expect. Since all genic combinations were homozygous in this experiment, no h components are involved—only d components and interactions between these additive components. The four replicates or groups were carried out at the same time and were randomised together. There is thus no point in taking out an item

for gross group or " block " effects. The groups differed in carrying similar but not identical recombinant chromosomes so that the variation of components and interactions over groups (item " replicates × (C+I) ") is of prospective interest.

The results are set out in tables 9 and 10. The most striking feature of table 9 is that, for the first time in these experiments, the effects of

TABLE 9

Analysis of variance of the fourth experiment. The entries in the body of the table are mean squares

Item	N	Females	Males
Components (C) . .	3	63·2†	96·0*
Res. interactions (I) . .	4	9·8	26·5
Replicates × (C+I) . .	6	90·8*	55·8*
Between cultures of like genotype	14	35·6†	11·7
Theoretical error . .	...	19·9	18·9

* $P<0{\cdot}01$. † $0{\cdot}01<P<0{\cdot}05$.

the segments are as significant in males as in females. There is no clear evidence of interaction from either sex, but the components vary from group to group in both. The empirical error variance, measured by variation between replicates of the genotypes, is significantly higher than the theoretical error in the females but not in males. The individual components of variation set out in table 10 are uninformative,

TABLE 10

Additive components of variation in the fourth experiment. The figures given are averages over the four replicates

	d_a	d_{p+q}	d_{r+d}	s.e.
Females . .	−1·16	0·37	−0·06	1·68
Males . . .	−0·98	−0·33	−1·09	1·32
Mean . .	−1·07	0·02	−0·57	1·49

except for their being of much the same size in both sexes, thus confirming the analysis of variance of table 9.

In setting these results into relation with those of the earlier experiments we must bear in mind that earlier the comparisons were chiefly among at least partly heterozygous combinations whereas this time they are among homozygotes. It may be therefore that the sex difference is mainly to be found in the behaviour of heterozygotes, variation among homozygotes showing up in one sex as much as the other. Comparisons among the viabilities of the homozygous males of the first experiment, however, reveals no expression of the differences which

are detectable between their sisters, and so lends no support to this possibility. It is possible, too, that the contrast with earlier experiments springs in part from variation, newly arisen by mutation during the time the chromosomes were stored between their construction and their use in this last experiment. That mutation had occurred is testified by the appearance of lethal homozygotes in this last experiment though obviously no lethals could have been present when the recombinant chromosomes were first made up. Whatever the cause of the contrast, the different structure of the experiment or mutation, it is clear that this last experiment adds little to our earlier evidence, especially to that from the first experiment.

5. THE GENETICAL ARCHITECTURE OF VIABILITY

Our information about the genetical architecture of viability must come chiefly from the first experiment: failure of cultures, differences in design and the narrower range of genetic differences followed, combine to make the second, third and fourth experiments less informative. So far as they go, however, they agree with the first one in the results they give except that none of them reveals genic interaction in an unambiguous way and the fourth shows differences in viabilities among males where no such differences appeared from any other experiment. The failure of interaction to appear clearly in the later experiments should not be regarded too seriously. There is a hint of its occurrence in the second experiment, where the mean squares depending on it exceed error in the females of both diallels (table 5). The third experiment is concerned with genetic differences confined to a very narrow region of the chromosome, and the fourth experiment again gives a hint of interaction among the males which here are revealing the effects of genic differences even more strongly than the females. The appearance of differences in viability among the males of the fourth experiment is a more positive disagreement with the earlier results. The reason for this occurrence is, however, obscure and it need not prevent us from discussing the genetical properties of the differences among the females upon which the first experiment throws most light.

Perhaps the most striking result of the experiment is this difference in the extent to which the sexes reveal the effects of genes mediating viability. This would be worthy of further study as a problem in its own right. It is not, however, our chief concern at present. Rather we wish to consider the genetical causation and structure of the character as we have found it. The first experiment (table 4) gives evidence of genetical activity of every segment of chromosome III, except segment C-c, in determining the viability of females. Furthermore segment D-d would appear to be acting in the opposite direction to its fellows in the sense that higher viability is associated with D, derived from the H chromosome, whereas with the other segments it is

associated with a, b and c from the L chromosome. Dominance is clear and, it would appear, complete. Also it is unidirectional towards high viability. Interaction occurs between the genes of different segments and the diallel analysis points to it being of a kind analogous to the " duplicate genes " of classical genetics with the dominant high viability genes of one segment tending to suppress, or at least reduce, the effects of low viability genes in the other segments.

One further point is made clear by this first experiment. The flies vary in the length of chromosome for which they are heterozygous. Some are homozygous for all of the four segments. Others are heterozygous for one segment, still others for two, three and even all four segments. The average viabilities of the different type of female are plotted against the number of segments for which they are heterozygous in fig. 4, the figures being obtained from the O1 and O2 diallels of the first experiment, in which the sexes were recorded separately. There is a tendency for viability to show a general rise as the number of heterozygous segments increases from one to three. But the flies heterozygous for all segments by no means show the greatest viability, nor do all the homozygous combinations show viabilities poorer than those of the majority of heterozygotes. In other words viability cannot be simply related to heterozygosity: gene content is the important consideration and not heterozygosity *per se*.

Now the genetical architecture of viability stands in sharp contrast to that of chaeta number as revealed by these same flies (Breese and Mather, 1957). Dominance was detectable in respect of chaeta number, but it was not so strong as with viability. Also it was ambidirectional and not unidirectional as with viability. There was evidence of interaction between the genes of different segments affecting chaeta number but again it was quite trivial in its effects as compared with the interaction of the genes affecting viability (fig. 2). The contrast of the additive or d, effects of the segments on chaeta number and viability is less instructive, since the uniformly greater chaeta producing activity of the H segments as compared with the L is to be attributed to the artificial selection applied for this character especially to the ancestors of the H line. We may note, however, that the relative magnitude of effect of the four segments are not the same for the two characters (fig. 3). Also it is perhaps significant, in view of the correlated response of fertility to selection for chaeta number observed by earlier authors (*e.g.* Mather and Harrison, 1949) that the segments from the L line gives higher viability in more cases than do segments from the H line which is descended from ancestors more heavily selected for chaeta number.

This contrast between the genetical architectures of chaeta number and viability is of interest in two respects. In the first place it shows us that the effects on the two characters cannot be attributed to any simple pleiotropic action of the same set of genes. The relative magnitudes and directions of the additive effects of the segments differ

for the two characters, as do their properties in dominance and interaction. To take the analysis further we have investigated the correlation between chaeta number and viability among the 28 genetic combinations in the females of diallels O1 and O2. The linear regression of viability (measured in angles) on abdominal chaeta number is −0·235 which has a probability of almost exactly 0·05. It is thus of marginal significance. It accounts for 14 per cent. of the overall variation in viability; and if we use differences between the reciprocals

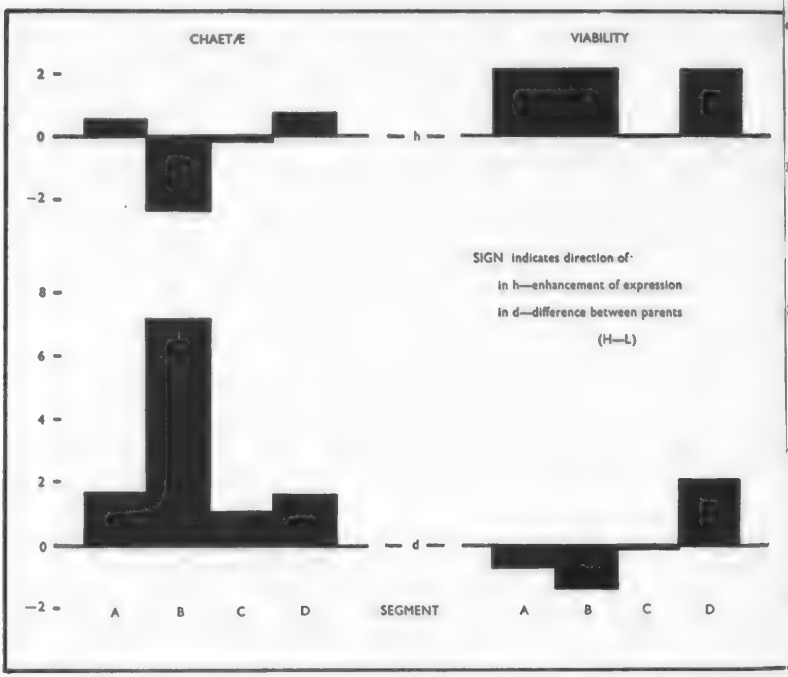

FIG. 3.—The contributions made by the four segments A-D (see fig. 1) to the additive (d) and dominance (h) variation in abdominal chaeta number and viability. All data are from the first experiment, those for chaetae being from the combined sexes in the whole experiment and those for viability from females in O1 and O2 only. The units of measurement are chaetae in the one case and angularly transformed percentage viabilities in the other.

of the crosses from which the 21 heterozygous combinations are derived as a measure of non-heritable variation, so arriving at an estimate of the heritable variation among the 28 genotypes we find that the correlation of chaeta number and viability still accounts for no more than 18·5 per cent. of the heritable variation in the latter. Thus even if we ascribe the whole of this relation between the characters to pleiotropic action of individual genes—an assumption which is by no means necessarily valid—we still have over $\frac{4}{5}$ of the heritable

variability in viability to account for by reference to further genes. Evidently simple pleiotropy is of but little help to us in understanding the relations between the genetic control of characters such as chaeta number and viability.

This is not to say that the pleiotropic action of genes is never of significance in determining the relations between characters or their correlated reponses to selection. Where characters are related developmentally in a reasonably simple way we must expect pleiotropic

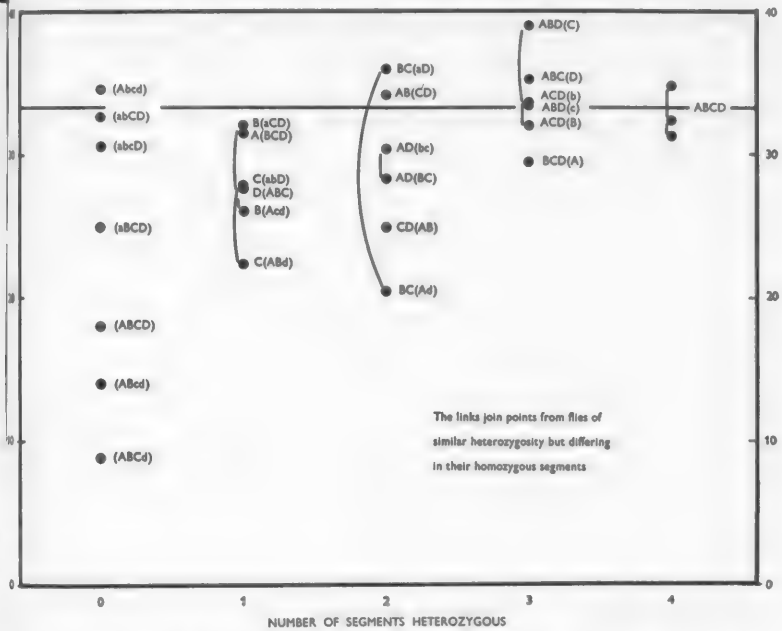

FIG. 4.—Viabilities of females in families from O1 and O2 of the first experiment plotted against the number of segments for which the flies were heterozygous. The segments for which the family was heterozygous are shown by unbracketed capital letters against each point and the homozygous segments by bracketed capital or small letters according to whether they came from H or L. All viabilities are in percentages, the horizontal line at 33⅓ per cent. marking the level at which the wild-type flies have a viability equal to their *Me Sb*/*H* sibs.

relations between them. Even in such cases, however, the pleiotropic tie may have far from simple consequences, as has been shown by Cocks (1954) in respect of the obviously relatable characters, abdominal and sternopleural chaeta numbers. When, therefore, we turn to such disparate characters as chaeta number and viability it is no surprise to find that pleiotropy of gene action is of little help in understanding their relations. Linkage of the members of the relevant polygenic systems is then the key to the determination of covariation within

related groups and correlated responses to selection. Such linkage will ensure that chromosome segments, or effective factors to use the term of Mather (1949), will show pleiotropic action even where the individual genes do not; but it will be a stable pleiotropy only so long as the chromosome segment is unbroken by crossing-over, for recombination will result in a redistribution of the linked associations and hence in a reassociation of the characters themselves. This conclusion is not new. The significance of linkage as opposed to genic pleiotropy, and the distinction between the apparent and resolvable pleiotropy of a segment or effective factor, which springs from linkage, and the unresolvable basic pleiotropy of single genes, have often been discussed and emphasised (*e.g.* by Mather and Harrison, 1949). The subject is raised yet again only because the present results hammer home so firmly the distinction between genes and segment and the insufficiencies of genic pleiotropy as an explanation of the relations observable between characters in genetical experiments.

6. GENETICAL ARCHITECTURE AND NATURAL SELECTION

The second respect in which the contrast between chaeta number and viability is of interest lies in the relation it reveals between the genetical architecture of a character and the forces of natural selection to which that character has been subjected (Mather, 1960). Now chaeta number and viability must be acted on differently by natural selection. Chaeta number would appear to have a central optimum with both extremes at a disadvantage relative to the more central values. In other words selection will be essentially stabilising. Viability on the other hand will obviously be subject more to directional selection, the advantage lying with the higher expression of the character.

It has been pointed out by Fisher (1930) that natural selection will tend to modify the phenotypic expression of heterozygotes towards closer resemblance to that of homozygotes carrying the more favourable allele. With unconditional advantage of one allele over another, such as would generally be the case where selection is essentially directional, this will mean unidirectional dominance as we have found with the viability genes. With stabilising selection, however, the more common allele will in the long run be the more favourable irrespective of the direction in which it pulls the character. Dominance should then tend to become ambidirectional (Fisher, *loc. cit.*) as is the case with the genes governing chaeta number. Thus the difference between the polygenic systems giving viability and chaeta number in respect of their properties of dominance is relatable to the difference in the impact of natural selection upon them.

The same difference might also be expected to arise in respect of non-allelic interaction. Directional selection would be expected to favour any interaction which tended to conceal the shortcomings in

action of the individual genes, and this is achieved by a duplicate system of interaction where dominance and interaction pull together, as we find it in the case of viability. With stabilising selection towards a central optimum the advantage of a given type and direction of interaction would vary with the combination of genes, so that there would be a lower and less persistent pressure of selection towards interaction and even such as evolved would tend to be ambidirectional and self-cancelling. Interaction should thus be a less striking feature of the gene systems governing a character of this type, and indeed in the case of chaeta number they appear to be so.

Studies in *Drosophila pseudoobscura*, *persimilis* and *prosaltans* have shown that interaction is as much a feature of the genetical architecture of viability in these species as in *D. melanogaster* (Spiess, 1958). And indeed we should expect it to be so as natural selection must be directional in its impact on viability in one species as much as in another. Spiess goes on further to point out the relation of the occurrence of so-called synthetic lethals to genic interactions. Such recombinational lethals would be expected with a duplicate type of interaction of the kind we have found, though we may note that complementary interactions, where homozygosity for one recessive gene produces the effect irrespective of the constitution at other loci, would not give them. This complementary relation is characteristic of the classical point mutation lethals, which serves again to emphasise the distinction between lethality springing from mutational and balance effects. Both types of lethal have been found in chromosome II of *D. melanogaster* (Misro, 1949), but surprisingly enough Hildreth (1956) has not been able to obtain evidence of synthetic or balance lethals in chromosome III. Spiess seeks to relate this to a difference in the properties of interaction in the polygenic systems of the two chromosomes as they affect viability, citing our own evidence that interaction of the genes in chromosome III is of little significance in the control of chaeta number. Even leaving aside the problem then raised of why the properties in interaction should differ between the gene systems of the two chromosomes, it is now clear that the difference in interaction is a feature not of the two chromosomes but of the two characters. Indeed certain of our observations positively suggest that such balance lethals do arise. In building up stocks for experiment 3 some 23 chromosomes were selected as showing recombination between *st* and p^b and 19 as showing recombination between p^b and *cu*. Two chromosomes for each set proved to be lethal when homozygous and, what is more, the lethals in the two *st*—p^b recombinants appeared to be allelic as did the two in the p^b—*cu* recombinants. The suggestion of a link between recombination and the appearance of lethals is clear. Our present data thus suggest that synthetic lethals are capable of production by recombination in chromosome III. So Hildreth's results are still unexplained and it would indeed appear worthwhile to repeat his experiments with other examples of chromosome III to discover whether his findings

were characteristic of this chromosome in general or merely specific to the sample of it that he happened to employ.

Differences in the genetical architecture of characters may be expected to show up when crosses are made between individuals from different populations, that is to say when combinations of genes are brought together which do not normally meet and which have therefore not been subjected to co-adaptation by the action of natural selection (Mather, 1943). With a relatively simple genetic system showing ambidirectional dominance such as is to be expected from the past action of stabilising selection and which has been found in the case of chaeta number, the relative unbalance of heterozygous genotypes resulting from crosses between individuals from different populations should show itself merely by increased average departure from the optimum. This departure is as likely to be towards lesser as towards greater manifestation of the character. In other words, inter-population hybrids should show a greater spread round their overall mean which itself need not depart from the mean of intra-population families. This spread must of course be measured as the variance of mean of families raised from inter-population crosses, since the variance within such families will chiefly reflect the degree of heterozygosity of the parents and so is largely irrelevant to the measurement of unbalance.

No data are available for chaeta number in crosses between wild populations of *D. melanogaster*, but the frequency of chiasma formation has been followed in such crosses of the campion plant *Lychnis dioica* by Dr C. W. Lawrence (see Mather, 1959). Chiasma frequency is a character with a central optimum and therefore subject to stabilising selection. Mr Lawrence has found an overall mean number of 14·07 chiasmata in the pollen mother cells of families raised from crosses within populations and an overall mean of 14·22 from crosses between populations. These two averages do not differ significantly. When, however, the variances were calculated among the family means, a figure of 3·6 was found for crosses between populations as against 1·15 for crosses within populations. This difference is in the expected direction and is significant. These figures differ a little from those quoted by Mather (1959) as a result of the addition of further material.

Observations are available on the viability of flies from inter-population crosses in a number of species of *Drosophila* (Vetukhiv, 1954, Wallace and Vetukhiv, 1955). The remarkable fact has emerged that viability is commonly higher in the F_1 of such crosses than in crosses made within populations, though in the F_2 it falls very much below the intra-population level. This result becomes much less surprising, however, when we consider the architecture of viability as we have found it. Dominance is unidirectional towards high viability, and in that it will be selected for in every population where the genes are segregating, we might expect it to be displayed as strongly or virtually as strongly in heterozygotes from crosses between populations as in

those from crosses within. Interactions will be selected only among genes occurring together and we might therefore expect them to be a less marked feature of genotypes obtained by crosses between, as opposed to within, populations. No clear information is available on this point. The mere occurrence of unidirectional dominance will, however, ensure that if the viability is maintained at its normal level by different polygenic combinations in different populations, the F_1 hybrids will enjoy the advantage of the genes from both populations and this will display itself as an even higher manifestation of the character. On this view the inter-population F_1's should be heterozygous for more viability genes than individuals within populations, and indeed would owe their greater viability to this higher heterozygosity. That they are in fact more highly heterozygous is attested by the great fall of viability in F_2, where the wider segregation and the lower effect of interaction between genes from different populations in maintaining viability will be making themselves felt.

The problem therefore resolves itself into the question of why populations should differ in the genes which maintain viability at its normal level. We should expect the genes varying and segregating in any one population to be but a sample of the full range of member genes of the polygenic system affecting viability, the rest of the genes being homozygous in that population. We should expect, too, that the genes varying in one population, or to put it the other way, the genes homozygous in one population, not to be the same as those in the other, if only for reasons of sampling. But why should the homozygous genes sometimes be the recessives making for lower viability, which will frequently be covered in inter-population F_1's, rather than always the dominant genes making for higher viability? The effects of any recessive genes tending to lower viability will of course be mitigated by their interactions, but they cannot have been wholly removed or the population flies would not be of lower viability than the inter-population hybrids. We must suppose, therefore, that even though viability within populations is not the highest that can be achieved, it is nevertheless adequate. While it would seem obviously to be true that higher viability will always have an advantage, it might well be that above a certain level the selective advantage does not rise correspondingly with the increase in viability as measured in experiment. Viability might then be stabilised at a level below the maximum by the operation of other factors within the population. Random fixation, such as must tend to occur within polygenic systems, would tend to result in at least some of the less advantageous genes becoming fixed and if the selective disadvantage were not great it could fail fully to counteract this tendency. In any case one thing is certain: the higher viability of the inter-population hybrids could not itself be stabilised within a population, for we have seen that it breaks down in F_2 as a result of segregation and recombination. High viability in one generation is not itself sufficient: it must be maintainable over

the generations. The behaviour of inter-population hybrids shows us that there can be a conflict between these requirements, for the genetic combination which gives the high expression of the character contains within its wide heterozygosity the seeds of its own breakdown. We must not be surprised, therefore, if we find the expression of a directionally selected character within a population to be not the maximum achievable but the maximum maintainable, and these are by no means necessarily the same thing.

7. SUMMARY

In the experiments described by Breese and Mather (1957) for investigating the distribution along chromosome III of polygenic activity affecting chaeta number, the wild-type flies whose chaeta were counted were obtained as parts of segregating families all of which contained $\frac{Me\ Sb}{H}$ flies. The proportion of wild-type flies relative to this constant marked class provides, therefore, a measure of the effect on viability of the various recombinant chromosomes that the wild-type flies carry.

In all but one of the experiments the females alone showed clear effects of the various recombinant chromosomes III on viability, the males showing little if any variation. For various technical reasons only the first of the experiments provides useful information about the genetical architecture of viability; and this shows dominance to be marked and unidirectional towards high viability. Non-allelic interactions of a kind relatable to the classical " duplicate gene " type are present and strong. Viability is not directly relatable to degree of heterozygosity.

The genetical architecture of viability is markedly different from that of chaeta number as revealed by the same flies in the same experiments. The simultaneous effects of the chromosomes on the two characters cannot be ascribed, except perhaps to a very small extent, to simple pleiotropy in action of the individual genes. Rather the pleiotropic effects of the chromosome segments are due to linkage within them of different polygenic systems affecting the two characters.

The differences in genetical architecture of the two characters are relatable to the different impacts of natural selection on them, selection for chaeta number being stabilising towards a central optimum and that for viability being directional towards an extreme value. The different expressions in inter-population crosses of characters showing the different architectures are reviewed and the occurrence in such F_1 hybrids of viabilities exceeding the levels found within populations is discussed. Viability within populations must be related to the maximum level maintainable which is by no means necessarily the maximum level achievable in any one generation.

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THE CORRELATIONS BETWEEN RELATIVES FOR A SEX-LINKED CHARACTER UNDER INBREEDING

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1. INTRODUCTION

THE method of analysing quantitative data by obtaining theoretical values for the correlations between relatives was developed by Fisher (1918). He derived expressions for correlations for different relationships under random mating. In recent years, the problem of correlations between relatives under inbreeding has aroused much interest in the field of quantitative inheritance as is evidenced by the papers of Horner (1956) and Kempthorne (1955). The particular form of inbreeding considered by Horner was the alternate parent-offspring mating and Kempthorne worked with the full-sib mating system. But in both these papers, the case of autosomal genes alone is dealt with, although under inbreeding, the progress towards homozygosis for a sex-linked character has long been studied by Fisher (1949) and Haldane (1937, 1955).

In this paper we have considered the case of a sex-linked character under full-sib mating system. The expressions for covariances between the four parent-offspring pairs, and the three full-sib pairs are derived. Some general expressions for the correlations between an individual and his/her offspring of k^{th} degree are derived under the assumption of no dominance, and the limiting values of these general expressions are discussed.

2. DEFINITIONS AND NOTATIONS

We consider here the case of one locus with two alleles, A and *a*. It is assumed that the female is homogametic, XX, and the male is heterogametic, XY, with respect to the sex-chromosomes. The frequencies for the six different mating types in the n^{th} generation with the offspring produced in the $(n+1)^{\text{th}}$ generation are given in table 1 below.

The frequencies in the $(n+1)^{\text{th}}$ generation are related to those in the n^{th} generation by the relation

$$\mathbf{L}^{(n+1)} = \mathbf{B}\,\mathbf{L}^{(n)} \tag{2.1}$$

where B is the matrix

$$\mathbf{B} = \begin{pmatrix} 1 & 0 & 0 & 0 & \frac{1}{2} & 0 \\ 0 & 1 & 0 & 0 & 0 & \frac{1}{2} \\ 0 & 0 & 0 & 0 & \frac{1}{2} & 0 \\ 0 & 0 & 0 & 0 & 0 & \frac{1}{2} \\ 0 & 0 & 1 & 0 & \frac{1}{4} & \frac{1}{4} \\ 0 & 0 & 0 & 1 & \frac{1}{4} & \frac{1}{4} \end{pmatrix} \tag{2.2}$$

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and $\mathbf{L}^{(n)}$ is the column vector

$$\mathbf{L}^{(n)} = \begin{pmatrix} L_1^{(n)} \\ L_2^{(n)} \\ L_3^{(n)} \\ L_4^{(n)} \\ L_5^{(n)} \\ L_6^{(n)} \end{pmatrix} \tag{2.3}$$

Such a matrix has already been considered by Fisher (1949) and Haldane (1955).

TABLE 1

No.	Mating type	Frequency in the n^{th} generation	Offspring produced in the $(n+1)^{th}$ generation				
			Male		Female		
			A	a	AA	Aa	aa
1	A×AA	$L_1^{(n)}$	1	...	1	...	...
2	a×aa	$L_2^{(n)}$	...	1	...	...	1
3	a×AA	$L_3^{(n)}$	1	...	...	1	...
4	A×aa	$L_4^{(n)}$	...	1	...	1	...
5	A×Aa	$L_5^{(n)}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	...
6	a×Aa	$L_6^{(n)}$	$\frac{1}{2}$	$\frac{1}{2}$	...	$\frac{1}{2}$	$\frac{1}{2}$

It is easily seen that the latent roots of (2.2) are 1, $\frac{1}{2}$, $-\frac{1}{2}$, ϵ, ϵ' and 1, where ϵ and ϵ' are the roots of the equation

$$4x^2-2x-1 = 0 \tag{2.4}$$

If initially the population was random mating and at equilibrium, *i.e.* the vector $\mathbf{L}^{(0)}$ is obtained by symbolically multiplying

$$(p\mathrm{A}+q\mathrm{a})(p^2\mathrm{AA}+2pq\mathrm{Aa}+q^2\mathrm{aa}) \tag{2.5}$$

where p is the frequency of the allele A, then following Fisher (1949), the genotypic array for the females in the n^{th} generation can be written as

$$\{p-pq(1-\mathrm{F}_n)\}\mathrm{AA}+2pq(1-\mathrm{F}_n)\mathrm{Aa}+\{q-pq(1-\mathrm{F}_n)\}\mathrm{aa} \tag{2.6}$$

and that for the males being

$$p\mathrm{A}+q\mathrm{a} \tag{2.6}^1$$

for all n.

It may be verified that the F_n used in (2.6) is the same as that used by Kempthorne (1955) for an autosomal gene, the initial conditions remaining the same. A similar result is given by Haldane (1937).

Let the genotypic values for the two sexes be coded as follows:

Sex	Genotype	Coded genotypic value
Female . .	AA	y_1
	Aa	$\frac{y_1-x_1}{2}$
	aa	0
Male . . .	A	y_2
	a	0

With these values, the means for the females and the males in the n^{th} generation, denoted by μ_n and μ'_n respectively are given by

$$\mu_n = py_1 - pqx_1(1-F_n)$$
$$\mu'_n = py_2$$

and similarly the variances are given by

$$V_n = \frac{(1+F_n)}{2} pqy_1^2 + \frac{(1-F_n)}{2} pqx_1^2 - (1-F_n)^2 p^2q^2x_1^2 + (1-F_n)pq(p-q)x_1y_1$$

$$V'_n = pqy_2^2.$$

3. PARENT OFFSPRING AND FULL-SIB COVARIANCES

Let the parent belong to the n^{th} generation and the offspring to the $(n+1)^{\text{th}}$ generation. Then, the expressions for the covariances for the four parent-offspring pairs are as given below:

(*a*) Cov (Father, son) $= F_{n+1}pqy_2^2$ (3.1)

(*b*) Cov (Mother, son) $= \frac{(1+F_n)}{2} pqy_1y_2 + \frac{(1-F_n)}{2} pq(p-q)x_1y_2$ (3.2)

(*c*) Cov (Father, daughter) $= \frac{(1+F_{n+1})}{2} pqy_1y_2 + \frac{(1-F_{n+1})}{2} pq(p-q)x_1y_2$ (3.3)

(*d*) Cov (Mother, daughter) $= F_{n+2}pqy_1^2 + \frac{(1-F_n)}{4} pqx_1^2 - (1-F_n)(1-F_{n+1})p^2q^2x_1^2 - [(\tfrac{1}{2})^n - (2-F_n-F_{n+1})] \frac{pq(p-q)}{2} x_1y_1$ (3.4)

It may be verified that (3.4) is the same as the parent-offspring covariance for an autosomal gene as given by Kempthorne (1955).

For full sibs in the $(n+1)^{th}$ generation, the covariances for the three full-sib pairs are as given below:

$$(e)\ \text{Cov (Full brothers)} = \frac{(1-F_n)}{2} pq y_2^2 \tag{3.5}$$

$$(f)\ \text{Cov (Brothers, sisters)} = F_{n+2} pq y_1 y_2 - [(\tfrac{1}{2})^{n+1} - (1-F_{n+1})] \frac{pq(p-q)}{2} x_1 y_2 \tag{3.6}$$

$$(g)\ \text{Cov (Full sisters)} = F_{n+2} pq y_1^2 - (1-F_{n+2}) pq x_1^2 - [(\tfrac{1}{2})^n - 4(1-F_{n+1})] \frac{pq(p-q)}{4} x_1 y_1 + (1-F_{n+1})[1-pq(1-F_{n+1})] pq x_1^2 \tag{3.7}$$

When $x_1 = 0$, *i.e.* there is no dominance, the correlation coefficients are as follows:

$$(a)\ {}_f\rho_s = F_{n+1}$$

$$(b)\ {}_m\rho_s = \left(\frac{1+F_n}{2}\right)^{\frac{1}{2}}$$

$$(c)\ {}_f\rho_d = \left(\frac{1+F_{n+1}}{2}\right)^{\frac{1}{2}}$$

$$(d)\ {}_m\rho_d = 2F_{n+2}(1+F_n)^{-\frac{1}{2}}(1+F_{n+1})^{-\frac{1}{2}}$$

$$(e)\ \rho_{b-b} = \frac{1+F_n}{2}$$

$$(f)\ \rho_{sib} = 2F_{n+2}\{2(1+F_{n+1})\}^{-1}$$

$$(g)\ \rho_{sis\text{-}sis} = 2F_{n+2}(1+F_{n+1})^{-1}$$

where ${}_f\rho_s$ = Corr. coeff. between father in the n^{th} generation and son in the $(n+1)^{th}$ generation;

and ρ_{b-b} = Corr. coeff. between two full brothers in the $(n+1)^{th}$ generation and so on.

The following inequalities are obtained from the above expressions,

1. $\rho_{sib} < {}_m\rho_d$
2. ${}_f\rho_d > {}_m\rho_s > \rho_{b-b} > {}_f\rho_s$.

4. GENERAL EXPRESSIONS

In this case, it is possible to find the expressions for correlation coefficients between parents in the n^{th} generation and the k^{th} degree offspring. We use the following notation:

X_n = Female parent in the n^{th} generation
Y_n = Male parent in the n^{th} generation
S_{n+k} = Male offspring of the k^{th} degree in the $(n+k)^{th}$ generation
D_{n+k} = Female offspring of the k^{th} degree in the $(n+k)^{th}$ generation.

We find the correlation coefficients under the assumption of no dominance.

(I) *Corr.* (Y_n, S_{n+k})

We first find the covariance. For this, it is necessary to find the probability that both Y_n and S_{n+k} are of genotype A.

Now, as Y_n is of the type A, we need only consider the matings of the type 1, 4 and 5 of table 1. Also, the probability of getting a male offspring of the type A for the six different mating types can be represented by the vector $(1\ 0\ 1\ 0\ \frac{1}{2}\ \frac{1}{2})$. Thus the probability that both Y_n and S_{n+k} are A can be written as:

$$P_1 = (1\ 0\ 1\ 0\ \tfrac{1}{2}\ \tfrac{1}{2})B^{k-1}(L_1^{(n)}\ 0\ 0\ L_4^{(n)}L_5^{(n)}0)' \qquad (4.1.1)$$

where B is the matrix (2.2).
Thus

$$\text{Cov}\ (Y_n, S_{n+k}) = P_1 y_2^2 - p^2 y_2^2 \qquad (4.1.2)$$

It may be noted that this as well as the subsequent results hold for $k = 1$ with $B^{k-1} = B^0 = I$, I being the unit matrix.

The correlation coefficients which can now be easily found for different values of k are given in table 2 below:

TABLE 2

K	1	2	3	4	5
${}_n\rho_k$	F_{n+1}	$\frac{1+F_{n+1}}{2}$	$\frac{1+3F_{n+1}}{4}$	$\frac{3+5F_{n+1}}{8}$	$\frac{5+11F_{n+1}}{16}$

It may be noted that ${}_n\rho_k$ satisfies the difference equation

$${}_n\rho_{k+2} = \tfrac{1}{2}[{}_n\rho_k + {}_n\rho_{k+1}] \qquad (4.1.3)$$

with

$${}_n\rho_1 = F_{n+1}$$

$${}_n\rho_2 = \frac{1+F_{n+1}}{2}$$

The general solution of (4.1.3) can be written as

$${}_n\rho_k = \frac{1+2F_{n+1}}{3} + (-\tfrac{1}{2})^k \frac{2(1-F_{n+1})}{3} \qquad (4.1.4)$$

For sufficiently large value of k, the second term in (4.1.4) may be neglected and we get

$${}_n\rho_\infty = \frac{1+2F_{n+1}}{3} \qquad (4.1.5)$$

(ii) *Corr.* (Y_n, D_{n+k})

Let

$$\left.\begin{aligned} P'_{11} &= \text{Prob}\,[Y_n = A;\ D_{n+k} = AA] \\ P'_{12} &= \text{Prob}\,[Y_n = A;\ D_{n+k} = Aa] \end{aligned}\right\} \tag{4.2.1}$$

Then we have

$$\left.\begin{aligned} P'_{11} &= (1\ 0\ 0\ 0\ \tfrac{1}{2}\ 0)B^{k-1}(L_1^{(n)}\ 0\ 0\ L_4^{(n)}L_5^{(n)}\ 0)' \\ P'_{12} &= (0\ 0\ 1\ 1\ \tfrac{1}{2}\ \tfrac{1}{2})B^{k-1}(L_1^{(n)}\ 0\ 0\ L_5^{(n)}L_4^{(n)}\ 0)' \end{aligned}\right\} \tag{4.2.2}$$

Hence

$$P'_{11}+\tfrac{1}{2}P'_{12} = (1\ 0\ \tfrac{1}{2}\ \tfrac{1}{2}\ \tfrac{3}{4}\ \tfrac{1}{4})B^{k-1}(L_1^{(n)}\ 0\ 0\ L_4^{(n)}L_5^{(n)}\ 0)' \tag{4.2.3}$$

Hence

$$\text{Cov}\,(Y_n, D_{n+k}) = [P'_{11}+\tfrac{1}{2}P'_{12}]y_1y_2 - p^2y_1y_2 \tag{4.2.4}$$

The correlation coefficients for different values of k are given below in table 3.

TABLE 3

K	1	2	3
${}_n\rho'_k$	$\left(\frac{1+F_{n+1}}{2}\right)^{\frac{1}{2}}$	$\frac{1+3F_{n+1}}{4} \times \left(\frac{1+F_{n+2}}{2}\right)^{-\frac{1}{2}}$	$\frac{3+5F_{n+1}}{8} \times \left(\frac{1+F_{n+2}}{2}\right)^{-\frac{1}{2}}$

In general, we have

$${}_n\rho'_k = ({}_n\rho_{k+1})\left(\frac{1+F_{n+k}}{2}\right)^{-\frac{1}{2}} \tag{4.2.5}$$

where ${}_n\rho_{k+1}$ is given by (4.1.4) with k replaced by $k+1$. Thus, for large k,

$${}_n\rho'_k \simeq {}_n\rho_{k+1}$$

$$\simeq {}_n\rho_k$$

as $F_{n+k} \to 1$.

(iii) *Corr.* (X_n, S_{n+k})

Let

$$\left.\begin{aligned} Q_{11} &= \text{Prob}\,[X_n = AA;\ S_{n+k} = A] \\ Q_{12} &= \text{Prob}\,[X_n = Aa;\ S_{n+k} = A] \end{aligned}\right\} \tag{4.3.1}$$

Then,

$$\left.\begin{aligned} Q_{11} &= (1\ 0\ 1\ 0\ \tfrac{1}{2}\ \tfrac{1}{2})B^{k-1}(L_1^{(n)}\ 0\ L_3^{(n)}\ 0\ 0\ 0)' \\ Q_{12} &= (1\ 0\ 1\ 0\ \tfrac{1}{2}\ \tfrac{1}{2})B^{k-1}(0\ 0\ 0\ 0\ L_5^{(n)}L_6^{(n)})' \end{aligned}\right\} \tag{4.3.2}$$

Hence

$$Q_{11}+\tfrac{1}{2}Q_{12} = (1\ 0\ 1\ 0\ \tfrac{1}{2}\ \tfrac{1}{2})B^{k-1}\left(L_1^{(n)}\ 0\ L_3^{(n)}\ 0\ \frac{L_5^{(n)}}{2}\ \frac{L_6^{(n)}}{2}\right)' \tag{4.3.3}$$

Hence,

$$\text{Cov}\,(X_n, S_{n+k}) = [Q_{11}+\tfrac{1}{2}Q_{12}]y_1y_2-p^2y_1y_2 \qquad (4.3.4)$$

Table 4 gives the correlation coefficients for different values of k.

TABLE 4

K	1	2	3	4
${}_n\eta_k \times \left(\frac{1+F_n}{2}\right)^{\frac{1}{2}}$	$\frac{1+F_n}{2}$	$\frac{1+F_n+2F_{n+1}}{4}$	$\frac{3+3F_n+2F_{n+1}}{8}$	$\frac{5+5F_n+6F_{n+1}}{16}$

As in (i), ${}_n\eta_k$ satisfies the difference equation

$${}_n\eta_{k+2} = \tfrac{1}{2}({}_n\eta_k+{}_n\eta_{k+1}) \qquad (4.3.5)$$

with

$${}_n\eta_1 = \left(\frac{1+F_n}{2}\right)^{\frac{1}{2}}$$

$${}_n\eta_2 = \frac{1+F_n+2F_{n+1}}{2}\times\left(\frac{1+F_n}{2}\right)^{-\frac{1}{2}}$$

The general solution of (4.3.5) can be expressed as

$${}_n\eta_k = \left[\left(\frac{1+F_n+F_{n+1}}{3}\right)-(-\tfrac{1}{2})^k\left(\frac{1+F_n-2F_{n+1}}{3}\right)\right]\left(\frac{1+F_n}{2}\right)^{-\frac{1}{2}} \qquad (4.3.6)$$

For large k, we may write

$${}_n\eta_\infty = \left(\frac{1+F_n+F_{n+1}}{3}\right)\left(\frac{1+F_n}{2}\right)^{-\frac{1}{2}} \qquad (4.3.7)$$

(iv) *Corr.* (X_n, D_{n+k})

Let

$$\left.\begin{aligned} Q'_{11} &= \text{Prob}\,(X_n = AA;\ D_{n+k} = AA)\\ Q'_{12} &= \text{Prob}\,(X_n = Aa;\ D_{n+k} = AA)\\ Q'_{21} &= \text{Prob}\,(X_n = AA;\ D_{n+k} = Aa)\\ Q'_{22} &= \text{Prob}\,(X_n = Aa;\ D_{n+k} = Aa)\end{aligned}\right\} \qquad (4.4.1)$$

Then,

$$\left.\begin{aligned} Q'_{11} &= (1\ 0\ 0\ 0\ \tfrac{1}{2}\ 0)B^{k-1}(L_1^{(n)}\ 0\ L_3^{(n)}\ 0\ 0\ 0)'\\ Q'_{12} &= (1\ 0\ 0\ 0\ \tfrac{1}{2}\ 0)B^{k-1}(0\ 0\ 0\ 0\ L_5^{(n)}L_6^{(n)})'\\ Q'_{21} &= (0\ 0\ 1\ 1\ \tfrac{1}{2}\ \tfrac{1}{2})B^{k-1}(L_1^{(n)}\ 0\ L_3^{(n)}\ 0\ 0\ 0)'\\ Q'_{22} &= (0\ 0\ 1\ 1\ \tfrac{1}{2}\ \tfrac{1}{2})B^{k-1}(0\ 0\ 0\ 0\ L_5^{(n)}L_6^{(n)})'\end{aligned}\right\} \qquad (4.4.2)$$

Hence

$$Q'_{11}+\tfrac{1}{2}(Q'_{12}+Q'_{21})+\tfrac{1}{4}Q'_{22} = (1\ 0\ \tfrac{1}{2}\ \tfrac{1}{2}\ \tfrac{3}{4}\ \tfrac{1}{4})B^{k-1}\left(L_1^{(n)}\ 0\ L_3^{(n)}\ 0\ \frac{L_5^{(n)}}{2}\ \frac{L_6^{(n)}}{2}\right)' \quad (4.4.3)$$

Then

$$\mathrm{Cov}\,(X_n, D_{n+k}) = [Q'_{11}+\tfrac{1}{2}(Q'_{12}+Q'_{21})+\tfrac{1}{4}Q'_{22}]\gamma_1^2-p^2\gamma_1^2 \quad (4.4.4)$$

Table 5 below gives the correlation coefficients for various values of k:

TABLE 5

k	1	2
${}_n\eta'_k \times \left(\frac{1+F_n}{2}\right)^{\frac{1}{2}}$	$\frac{1+F_n+2F_{n+1}}{4} \times \left(\frac{1+F_{n+1}}{2}\right)^{-\frac{1}{2}}$	$\frac{3+3F_n+2F_{n+1}}{8} \times \left(\frac{1+F_{n+2}}{2}\right)^{-\frac{1}{2}}$
k	3	4
${}_n\eta'_k \times \left(\frac{1+F_n}{2}\right)^{\frac{1}{2}}$	$\frac{5+5F_n+6F_{n+1}}{16} \times \left(\frac{1+F_{n+2}}{2}\right)^{-\frac{1}{2}}$	$\frac{11+11F_n+10F_{n+1}}{32} \times \left(\frac{1+F_{n+4}}{2}\right)^{-\frac{1}{2}}$

In general

$${}_n\eta'_k = {}_n\eta_{k+1}\left(\frac{1+F_{n+k}}{2}\right)^{-\frac{1}{2}}$$

where ${}_n\eta_{k+1}$ is given by (4.3.6) with k replaced by $k+1$. For large k, we have

$${}_n\eta'_k \simeq {}_n\eta_{k+1} \simeq {}_n\eta_k$$

as $F_{n+k} \to 1$.

5. DISCUSSION

It is noted that because of the particular initial conditions, the latent root $-\frac{1}{2}$ does not appear at all in any of the expressions.

The covariance between mother and daughter for a sex-linked case and that between parent-offspring for an autosomal case is found to be the same. This is to be expected, since the segregation in the female is the same either for sex-linked or autosomal characters.

It is interesting to note from section 4 that the limiting values of the correlations between an individual and his/her k^{th} degree offspring do not depend on the sex of the offspring, the limiting value, as k becomes larger, being the same.

6. SUMMARY

In this paper expressions for correlations between parent-offspring and full-sib pairs are derived for a sex-linked character under full-sib mating system. General expressions for correlations between an individual and his/her offspring of the k^{th} degree are also derived assuming no dominance. The results obtained are briefly discussed. The case of a single locus with two alleles affecting the sex-linked character alone is considered.

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DEVELOPMENTAL STABILITY IN CONSTANT AND FLUCTUATING TEMPERATURES

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1. INTRODUCTION

THE comparative study of different genotypes has to be carried out in controlled environments, and for convenience, such conditions are usually made as constant as possible. Under natural conditions, however, many biological populations are exposed to variations both in time and space and must be adapted to survive such variations. Information as to the effects of fluctuating environments on individuals and populations is clearly desirable.

Regular fluctuations with periods greater than generation time may provoke characteristic cyclic changes in the gene pools of populations (Dobzhansky, 1950; Dubinin and Tiniakov, 1945; Timoféeff-Ressovsky, 1940). On the other hand, both regular and irregular fluctuations of short period must be met by the individual's developmental homeostasis (Lerner, 1954), developmental stability (Mather, 1953) or developmental flexibility (Thoday, 1953) and it might therefore be expected that the genotypes best adapted to constant conditions would be genetically different from those best adapted to fluctuating conditions. Very few informative comparisons have been made in this connection but suggestive results have been obtained by Tebb and Thoday (1954*a*, *b*). It therefore seemed worth while to compare the developmental stability or homeostasis of different *Drosophila* genotypes in constant and fluctuating temperature conditions.

2. MATERIALS AND METHODS

(i) *The environments*

Tebb and Thoday, 1954*a*, *b*, obtained a diurnal fluctuation of temperature by moving their cultures from one constant temperature room to another each morning and evening. Apart from the labour, this system has the disadvantage that the precise mean temperature is not easily controlled. An incubator which produced a fluctuating temperature that would be relatively precisely controlled was therefore designed and built.

This incubator provided an environment, which will be termed F20°/30°, with a mean temperature of 25° C. The temperature at midday was 30° C. and that at midnight 20° C. Fig. 1 shows a typical recording from a thermograph in the incubator.

The fluctuation was produced by a clock that revolved once each 24 hours. The clock was connected to the thermostat control by a crank system so that the revolution of the clock caused oscillations of the thermostat spindle and hence diurnal fluctuation of temperature. In practice this mechanism worked very well although theoretically the type described by Howe (1956) is probably preferable.

For most of the work (but see below, ii) the constant temperature environment was provided by a water-jacketed incubator maintained at 25° C. Humidity in both incubators was maintained in the range 35-50 per cent. R.H. and the observed diurnal oscillation of relative humidity in F20°/30° rarely exceeded ±4 per cent. in the air surrounding the cultures. Within the culture bottles it would presumably be even less.

(ii) *Stocks of* Drosophila melanogaster

In the first group of experiments, cultures of the highly inbred stocks Oregon and Samarkand and of their crosses were raised in the constant and in the fluctuating environments. Each culture was derived from a double pair mating. Five replicates per genotype were grown in each experiment. There were eight nominally replicate experiments, but these differed slightly. For experiments 1-4 a culture room ostensibly maintained at 25° C. but with appreciable variations in temperature was

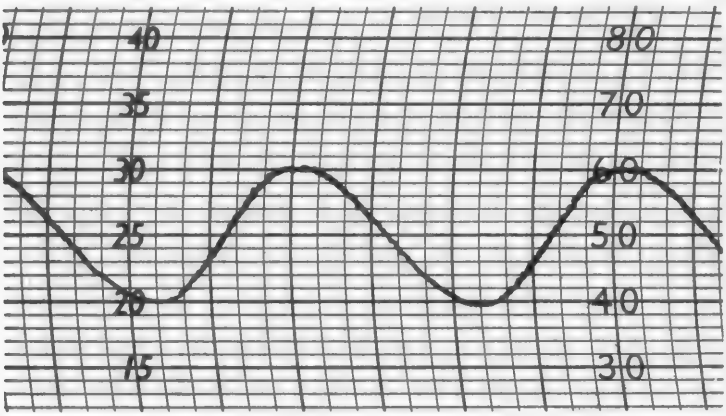

FIG. 1.—Thermograph recording taken in the fluctuating temperature incubator.

used to provide the 25° C. environment. An accurately controlled incubator maintained at 25° C. was available for the later experiments.

In the second group of experiments two " wild " stocks were used, each descended from an inseminated female, one taken at Bayfordbury and one at Sheffield (Bannerdale). Five replicate cultures of each of the two stocks and the two reciprocal crosses were grown in each experiment, each culture being derived from a single pair of parents.

(iii) *The index of homeostasis*

The index of homeostasis in the present study was essentially that used by Mather (1953), Tebb and Thoday (1954*a*) and Thoday (1958), asymmetry of sternopleural chaeta number. Despite criticisms (*e.g.* Waddington, 1958) there now seems to be little doubt that this character is a useful, if limited, index of developmental homeostasis. The results of Mather (1953), Tebb and Thoday (1954*a*), Beardmore (1956) (quoted in Thoday, 1958), Beardmore, Dobzhansky and Pavlovsky (1960), are consistent in indicating some negative correlation between asymmetry and Darwinian fitness. A discussion of the value of this character will be found in Thoday (1958).

3. RESULTS

(i) *The inbred stocks and their F_1's*

Table 1 shows the mean asymmetry per 20 flies of sternopleural chaeta number for the two inbred lines, O and S, and for the two reciprocal F_1's in the 25° C. and F20°/30° environments. These mean values are based on the total data from the eight experiments. In the analysis of variance of the asymmetry data (table 2) only the data

TABLE 1

Asymmetry of sternopleural bristle number in O, S and their F_1's in two environments (each entry represents the summed asymmetry of 20 flies averaged over 80 cultures with the sexes combined)

Environment	Genotype					
	O	S	Mean P	O×S	S×O	Mean F_1
Constant 25° C. .	21·22	17·52	19·36	18·12	18·32	18·22
Fluctuating 20°/30° .	20·20	18·44	19·22	20·20	19·66	19·92

from the last four of these experiments have been analysed, for only in these experiments was the temperature properly controlled.

The first item in the analysis of variance set out in table 2 is very highly significant and indicates differences between genotypes. This when partitioned proves to be largely the result of difference in mean

TABLE 2

Analysis of variance of asymmetry in two inbred lines and their F_1's in two environments

Item	d.f.	Mean square	P
Genotypes	3	89·40	<0·001
Environments	1	47·30	>0·05
Environments × Genotypes . .	3	54·89	<0·01
(Env. × PF_1	1	149·9	<0·001)
Environment × Sex . . .	1	79·00	<0·02
Error	258	13·29	

asymmetry between the O and S parents, the O stock being characterised by a higher asymmetry than the S stock. This is quite possibly a result of a difference in sternopleural bristle number, T, rather than developmental stability, for in general, though not always (Mather, 1953), flies with more bristles are also more asymmetrical. Table 3 shows the mean T for hybrid and inbred genotypes in both environments and the value of T for O is appreciably greater than that for S.

A significant interaction between genotypes and environment is shown in the analysis (table 2). Of the total sum of squares for three degrees of freedom, by far the greatest part is absorbed by the one degree of freedom available for comparing the combined parents with the combined F_1's in the two environments. This $PF_1 \times$ environment interaction is significant as well below the 0·001 level of probability.

TABLE 3

Mean sternopleural bristle number (T) in O, S and their F_1's in two environments (sexes combined, each entry is the mean of 1600 flies)

Environment	Genotype					
	O	S	Mean P	O×S	S×O	Mean F_1
Constant 25° C. .	19·33	16·83	18·08	18·24	17·59	17·91
Fluctuating 20°/30° .	19·32	16·69	18·07	18·04	17·23	17·63

If the data are divided and separate analyses carried out for each environment, it is found that the F_1's are significantly less asymmetrical than the parental types in 25° C. but not in F20°/30°. The interaction in the analysis of the total is therefore a result of this relative difference of behaviour of the inbreds and F_1's in the two environments. The $PF_1 \times$ environment interaction cannot plausibly be attributed to simple

TABLE 4

Mean number of flies hatching per 10 eggs in O, S and their F_1's in two environments (each entry is the mean of 40 cultures)

Environment	Genotype					
	O	S	Mean P	O×S	S×O	Mean F_1
Constant 25° C. .	5·60	5·40	5·50	8·00	6·22	7·11
Fluctuating 20°/30° .	5·54	5·57	5·56	7·25	6·22	6·73

changes in chaeta number T. Although as shown in table 3, T is in general slightly, but significantly lower in F20°/30° than 25° C., the observed differences in T cannot alone be responsible for the relative differences in asymmetry of hybrids and inbreds under constant and fluctuating conditions.

The egg-eclosion viability of the inbred lines and their F_1 hybrids in the two environments is given in table 4. The viability of the hybrids is greater than that of the parental types, and the difference between P and F_1 viability is statistically significant in both environments ($P = < 0{\cdot}001$).

(ii) *The wild stocks*

The first experiment with the wild stocks involved testing the developmental homeostasis of the descendants of two wild gravid females, two generations after the initial capture. Tests were made in both environments. Both the stocks and the two F_1 crosses between them

TABLE 5

Mean asymmetry (per 20 flies) of sternopleural bristle number in two wild strains and their F_1's

Experiment	Genotype	Environment	
		25°	F°
I	Bannerdale	16·6	14·8
	Bayfordbury	23·0	20·6
	Bannerdale × Bayfordbury	18·7	17·4
	Bayfordbury × Bannerdale	19·1	18·1
II	Bannerdale	17·7	18·5
	Bayfordbury	21·2	21·2
	Bannerdale × Bayfordbury	19·4	19·8
	Bayfordbury × Bannerdale	19·5	20·1

were tested and the results are shown in the upper part of table 5. All genotypes are characterised by *lower* asymmetry in the fluctuating environment than in the constant environment and this difference is statistically significant ($P = < 0{\cdot}05$).

TABLE 6

Analysis of variance of asymmetry in two wild strains and their F_1's in two experiments

Item	d.f.	Mean square	P
Experiments	1	51	$< 0{\cdot}02$
Environments	1	13	$> 0{\cdot}20$
Genotypes	3	142·3	$< 0{\cdot}001$
Experiments × Environments	1	44	$\simeq 0{\cdot}02$
Experiments × Genotypes	3	16	$> 0{\cdot}2$
Experiments × Sex	1	11	$> 0{\cdot}2$
Error (pooled)*	149	8·48	

* The error mean square is based upon a sum of squares which includes the variance between cultures and those items not listed in the table whose individual mean squares were similar to the original error mean square.

The second experiment with these stocks was carried out in the same way as the first, but ten months later. The stocks had been maintained in the intervening period in mass culture under normal laboratory conditions at 25° C. The mean asymmetry for the four genotypes in the two environments is shown in the lower half of table 5.

Though there is an obvious suggestion that flies cultured in the fluctuating environment are now *more* asymmetrical than those cultured at 25° C., in fact the difference is not significant, $P > 0{\cdot}05$.

An analysis of variance of the combined data from the two experiments is shown in table 6. There are significant items due to experiments, genotypes and the experiments × environments interaction. The genotypes item is a reflection of the fact that, as with the O and S stocks, the Bayfordbury and Bannerdale stocks have different mean asymmetries largely because they have different total bristle numbers. The F_1's have intermediate values of both asymmetry and T. The experiments × environment item arises because the mean asymmetry in F20°/30° was higher in the second experiment than in the first, the asymmetry values in 25° being more or less similar in the two experiments. It is this which is responsible for the experiments item.

The interaction may be interpreted as follows. In the first experiment all genotypes showed greater developmental stability in F20°/30° than in 25° C. but in the second experiment developmental stability was lower, though not significantly so, in the fluctuating than in the constant environment (see fig. 3).

4. DISCUSSION

(i) *The inbred stocks and their F_1's*

In the 25° C. environment, the developmental stability of the F_1's between the two inbred lines O and S, as measured by asymmetry of sternopleural chaetæ, is superior to that of the inbreds. This agrees with Mather's (1953) findings. In the fluctuating condition, however, the hybrids are at least as unstable in development as the inbred types (fig. 2). This is a somewhat surprising result for there is no obvious reason why the F_1 superiority should not be retained in the fluctuating environment. There are two hypotheses, not necessarily mutually exclusive, that might explain this result. The first hypothesis assumes that a change of environment may produce a change in dominance relations of the type postulated by Lewis (1953). Using his model any phenotypic character affected by given environmental changes would display a variance in F_1 hybrids which would be greater or less than that of the parents depending on whether the genes affected worked in the same direction as the environment or in the opposite direction. Applied to this experiment the model would require that during part or all of the high temperature half of the fluctuating temperature cycle (tending to reduce chaeta number), minus chaeta-number genes are on average dominant to their plus alleles in F_1 flies. Conversely, during the colder half (increasing chaeta number) plus genes would be dominant to minus genes. Such a response could well be adaptive, for there is evidence (Beardmore, 1956; see Thoday, 1958) that low chaeta number at high temperatures and high chaeta number at low temperatures may be adaptively useful. Now as chaeta number

determination seems to occur over a period of time (Plunkett, 1927) it is likely that a dominance change of the type postulated would have two consequences. These are an increased variance of F_1 chaeta number in F20°/30° and increased F_1 asymmetry in F20°/30°. The first of these consequences follows because unless the period of time during which chaeta number is determined is for all flies an exact multiple of the wavelength of the temperature oscillation, different flies will inevitably suffer different temperature experiences and produce

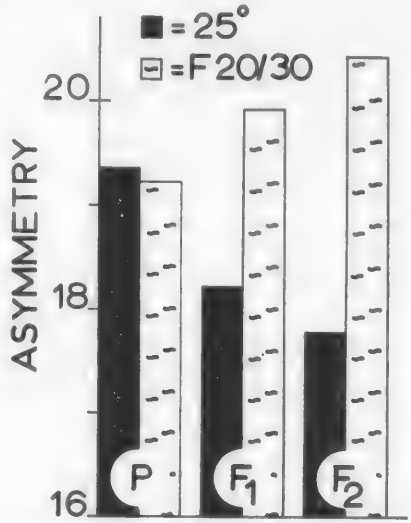

FIG. 2.—Mean sternopleural asymmetry per 20 flies of the inbred lines Oregon and Samarkand, their F_1's and F_2's in a constant and in a fluctuating environment.

different chaeta numbers. Similarly, unless chaeta production on the two sides of a fly were perfectly synchronous, an increase in asymmetry would result from the two sides developing at different temperatures. When the variance of chaeta number (T) in F20°/30° is examined it is found that (compared with 25° C.) it is increased in *both* F_1 and parental genotypes (table 7). This increase, assuming it results from the same cause in both P and F_1, cannot be due to a change in dominance. This evidence, therefore, does not support the dominance hypothesis unless it be supposed that the increase in variance is produced by different means in the inbreds and F_1's.

One further point requiring discussion is the difference observed between asymmetry and viability as indices of homeostasis in the two environments. The hybrids are more viable than the inbreds in both environments and clearly (table 4) there is no hint of a dominance change, though as viability can only vary adaptively in one direction, a dominance change would perhaps not be expected.

The alternative hypothesis is that, as the reversal of relative homeostasis is due primarily to the hybrids being absolutely less homeostatic in F20°/30° than in 25° C., the superiority of the F_1's in 25° C. arises not from heterosis alone but also because the F_1 combines genomes derived from parents both long adapted to constant 25° C. hence are themselves adapted to these conditions and when put together co-operate more successfully in 25° C. than in F20°/30°. Once more

TABLE 7

Coefficient of variation of sternopleural chaeta number in O, S and their F_1's in two environments

Genotype	Environment					
	25° C.			F20°/30°		
	♀	♂		♀	♂	
O . .	6·94	7·72		10·50	10·26	
S . .	7·44	7·42		10·99	10·60	
Mean P .			7·38			10·58
O×S .	6·91	7·45		10·38	11·22	
S×O .	6·82	6·87		10·75	10·79	
Mean F_1 .			7·00			10·79

the fact that the hybrid genotypes are more viable than the inbreds in both environments and the difference between the responses of asymmetry and viability must be considered. This difference may suggest that asymmetry cannot have any adaptive significance for the importance of viability as a component of Darwinian fitness is obvious. It is important to remember, however, that natural selection works upon the totality of the phenotype. Thus different phenotypic characters in an organism will always be at different distances from their respective optima depending both upon the relative adaptive importance of the character and upon the interactions between characters. In outbreeding species, natural selection should act in such a way as to favour the establishment of the maximum possible number of gene combinations which will produce the optimal phenotype. When different phenotypic characters are considered it will be clear that in general the number of such combinations is likely to be positively correlated with the relative importance of the character in tota Darwinian fitness. Thus it is likely to be very high for viability; as Wallace (1957) has shown, most increments of randomly produced

heterozygosity to a homozygous system improve viability. In the case of morphological characters the number of combinations is likely to be greater for genes mediating say symmetry in eye development than for those concerned with symmetry in sternopleural bristle development, for this may be presumed to be of a lower order in the scale of adaptive value than the former. Robertson (1955, 1959) discussing the relationship between fitness, genetic variance and various phenotypic characters in equilibrium populations arrived at a similar conclusion. This argument may be extended to include change of environment as well as change in genotype, the character of lesser adaptive significance being more (unfavourably) affected than the one of greater significance, when the environment changes. In the present study we may conclude that the loss of F_1 heterosis in terms of symmetry and its maintenance in terms of viability in F20°/30° are related to this.

The F_2 generation from crosses between O and S was shown by Mather (1953) to be less asymmetrical at 25° C. than the F_1's although less heterozygous. A small number of F_2 cultures grown in the present study produced data in agreement with this although the difference between F_1 and F_2 is not statistically significant (see fig. 2). More interesting is the fact that the F_2 flies in F20°/30° are ostensibly, though again not significantly, more asymmetrical than the F_1's. This may perhaps be taken to mean that not only are the F_2's in 25° nearer to an optimal state of heterozygosity than are the F_1's (as suggested by Thoday in Mather, 1953), but that the relational balance (Mather, 1943) in F_2 is specific or at least not general enough to give good homeostasis in F20°/30°. This may again be a consequence of the maintenance of the inbred parents in constant 25° C. for several hundred generations.

Although the argument advanced above should not perhaps be accepted without reserve the results appear to favour the second hypothesis rather than the first. They also provide another demonstration that heterozygosity as such does not inevitably lead to superior homeostasis although the validity of this statement depends upon the definition of homeostasis. A more important point is that these data emphasise the illegitimacy of extrapolating conclusions concerning fitness from one environment to another.

(ii) *Wild stocks*

The test with wild stocks showed that flies two generations removed from populations in the wild state showed a greater asymmetry in a constant temperature than in a fluctuating temperature. After approximately fifteen generations under normal laboratory conditions the populations were equally asymmetrical in both environments (fig. 3). This may be interpreted as meaning that the removal, for fifteen generations, of selection for adaptation to fluctuating conditions had resulted in some breakdown of the gene complexes established under such selection pressures in the wild. It would then, of course, be expected that adaptation to constant temperature conditions should

improve over the fifteen-generation period. Because of differences in T (and hence in asymmetry) between the two experiments it is difficult to be sure whether adaptation does so increase. The value of T showing the smallest between-experiment difference is that of the Bayfordbury stock and in this stock, adaptation to 25° C. as measured by asymmetry does improve between the two experiments. Though this difference is not statistically significant, the rather few data are ostensibly in agreement with the idea of adaptation and asymmetry being negatively correlated.

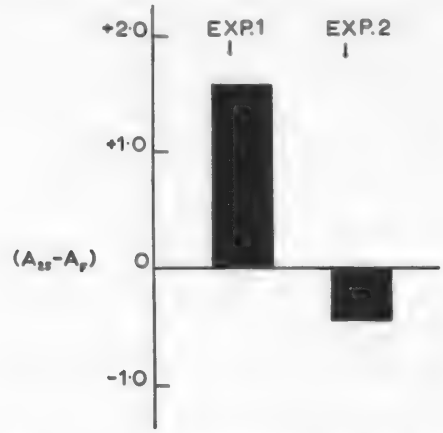

FIG. 3.—Mean difference per 20 flies of sternopleural asymmetry of "wild" strains in constant (A_{25}) and fluctuating (A_F) temperatures in two experiments.

Irrespective of the precise interpretation that may be placed upon these results it is clear that natural populations of *Drosophila* possess gene complexes capable of buffering development within a diurnally varying thermal environment and that such complexes are not necessarily capable of buffering development equally well under conditions of thermal stability*, to cope with which new gene complexes must be built up (*cf.* Bishop (1953) who observed 100 per cent. increase in the hatchability of eelworm cysts in fluctuating compared with constant temperature). The building-up of such genetic architecture seems to be essentially an adaptive process (Beardmore, 1956). These results, therefore, show that appreciable modifications of the gene pools of populations may occur when they are kept under laboratory conditions. The experiments with the inbred lines demonstrated that a difference between inbred and hybrid genotypes clearly shown at 25° C. disappeared under conditions of fluctuating temperature. Tests of wild chromosomes in constant laboratory conditions might in the same way give results which are not predictive of the attributes

* Note added in proof. Ford (in *Moths*, Collins 1955, p. 57) quotes the work of Kettlewell on body colour mutants of *Panaxia dominula* L. in which a similar situation may exist.

of such chromosomes in natural environments. Together these findings should engender caution in considering the relevance to wild populations of laboratory data.

5. SUMMARY

1. The developmental homeostasis of the inbred lines, Oregon and Samarkand of *Drosophila melanogaster* and of their F_1 hybrids, was studied in thermally constant (25° C.) and diurnally fluctuating environments (F20°/30°) of the same mean. Similar investigations on wild strains were also carried out.

2. In the constant temperature, homeostasis as measured by the mean asymmetry of the sternopleural chaetæ was greater in the F_1 hybrids than in the inbred lines Oregon and Samarkand, confirming Mather's (1953) results. The F_1's also showed heterosis in egg-adult viability. In the fluctuating environment the F_1's were no more homeostatic (symmetrical) than the inbreds but were significantly more viable. The fact that F_1's are more symmetrical than their inbred parents in constant 25° C. than in F20°/30° can be accounted for by (i) the dominance of genes affecting chaeta number varying in the fluctuating environment or (ii) better co-operation between the two halves of an F_1 genotype in constant than in fluctuating conditions consequent upon both halves being derived from parents themselves long adapted to constant 25° C. conditions.

The contributions of bilateral symmetry and egg-adult viability to total Darwinian fitness are of different order, the symmetry component being smaller (though not negligible). This difference is reflected in the number of genetic combinations giving the desirable phenotype for each character and in the response of particular genotypes in different environments.

3. Second generation descendants of two wild-captured inseminated females of different origin and crosses between these displayed less bilateral asymmetry under fluctuating temperature conditions than under constant temperature. After fifteen generations in the laboratory this difference was no longer evident in descendants of the wild flies. Hence wild populations are presumed to carry gene complexes buffering development under conditions of fluctuating temperature. Such genetic architecture is a product of natural selection and appears to be destroyed in populations maintained under constant temperature conditions.

4. Taken together these results indicate the necessity for caution in predicting what may happen in natural populations from laboratory data.

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DIVERGENT EFFECTS OF NATURAL SELECTION ON TWO CLOSELY-RELATED POLYMORPHIC SNAILS

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1. INTRODUCTION

THE shells of land snails of the genus *Cepaea* Held. display striking colour and banding polymorphisms which have attracted the attention of many workers, particularly as supposed examples of random variation. Cain and Sheppard (1954) have shown, however, that the proportions of different varieties in colonies of *Cepaea nemoralis* L. can be related to the colour and uniformity of the background. They explain this relation, but not the maintenance of the polymorphism itself, in terms of selective visual predation, which has been demonstrated by Sheppard (1951).

Lamotte (1951) admits the existence of visual selection, but regards it as unimportant. The most cogent of his arguments is that he can find no correlation between the variations in *C. nemoralis* L. and *C. hortensis* Müll. living together in mixed colonies. The two species are almost identical in appearance, show a similar range of phenotypes, and seem to share the same predators. Lamotte reasons that if visual predation were important in determining the proportions of phenotypes, the two species should show parallel variation. They do not. Cain and Sheppard argue that this result does not necessarily contradict their hypothesis. The consequences of visual predation may be influenced by the non-visual selective values of the various phenotypes, values that are unlikely to be the same in both species. Small differences in ecology or behaviour might also result in a different pattern of selection, even from the same predator.

The work described in this paper is a study of the distribution of phenotypes in natural populations of *Cepaea hortensis* and an attempt to make clear the differences between its polymorphism and that of *Cepaea nemoralis*.

2. METHODS

During 1957 and 1958, I collected random samples of *C. hortensis* from sixty-four colonies, most of them within sixty miles of Oxford. Localities were selected for diversity of vegetation and background. Where possible, several widely separated habitats of the same type were studied. During sampling the area was searched carefully to avoid collecting only those snails that were most obvious to the eye.

The snails were scored for age, condition (live, dead predated, or dead unpredated), colour and banding :—

(1) Age

Snails whose lips had not yet formed were classed as juveniles. Those with complete or incomplete lips were considered to be adult.

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(ii) *Condition*

In order to prevent duplication, broken shells were scored only if they displayed more than half the lip. Shells broken by thrushes could usually be distinguished from those predated by small mammals (see Morris, 1954).

(iii) *Colour*

In *C. hortensis* the colour of the shell varies from almost pure white to a very dark greenish-black, but the commonest colours are white, yellow, pink and brown (see Taylor, 1914). The first two colours (var. *alba* Picard and var. *lutea* Picard) are often difficult to separate, and appear to have every sort of intermediate between them. I have included them both in the " yellow " class. The pink forms (var. *incarnata* Picard) and the " browns " (var. *baudonia* Moquin-Tandon and var. *olivacea* Taylor) can more easily be distinguished. Shells of the latter group have a pale violet ground-colour which is modified by the overlying periostracum so that they appear brown. It is probable that Taylor's var. *lilacina* is a brown that has a very pale periostracum.

(iv) *Banding*

The shell may have up to five bands running along the whorls (very rarely six or more). The bands are usually dark brown in colour. A form in which they

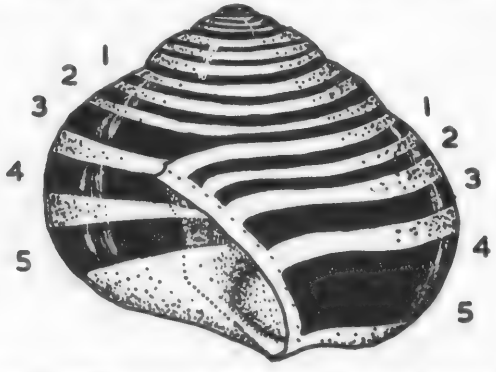

FIG. 1.—A shell of *C. hortensis*, showing the method of numbering the bands. On the right-hand whorl, bands 4 and 5 are fused.

are translucent and unpigmented on a pale yellow or white ground-colour (var. *arenicola* MacGillivray) occurs among my collections, usually as a distinct type. In some samples, however, there is a general tendency for the bands to be pale or partially pigmented (var. *lurida* Moquin-Tandon), and intermediates occur between normal banding and the unpigmented condition. Collections showing more than 10 per cent. of such forms are recorded with an asterisk, but the individual shells, unless completely unpigmented, are scored as normal.

For recording, the bands are numbered 1, 2, 3, 4 and 5 from the top of the whorl downwards (see fig. 1). Absence of a band is recorded by 0, and fusions are signified by bracketing the numbers representing the fused bands (*e.g.* (12)3(45), 023(45) etc.). Following Cain and Sheppard (1950) I have not regarded bands as fused unless they are joined for at least 90° round the whorl from the lip. Fusions are not scored in young snails. Bands occurring only as a faint trace near the lip are not recorded as present. They are very rare.

I have grouped the habitats from which samples were taken into six classes.

(i) *Grass*. This includes open chalk downlands as well as a number of roadside habitats in which grass predominates. The background is usually a uniform light green. In long grass it may be darker, but still fairly uniform.

(ii) *Hedgerows and rough herbage*. This class comprises open roadside habitats in which grass does not predominate. The vegetation is often mixed, and may include nettles (*Urtica dioica* L.), brambles (*Rubus* sp.), willowherb (*Epilobium* spp.), ivy (*Hedera helix* L.), hawthorn and various umbellifers. The background is generally darker and less uniform than in the grassy habitats.

(iii) *Beechwoods*. These are all escarpment woods of pure beech, or beech and ash. *C. hortensis* is not common within them, but tends to occur where there is some ground vegetation. The collections from Maidensgrove and Savernake were taken in patches of rosebay willowherb (*Epilobium angustifolium* L.), those from Clipper Down, Hackpen and Aston Rowant in stinging nettles, and the Ward's Hurst sample was collected from low brambles. The Knoll Down group are small beech clumps—each less than a hundred yards across, and each surrounded by downland grass. At Knoll Down B the ground flora within the clump itself is predominantly grass. There is less grass at Knoll Down A, and hardly any at all in Knoll Down C. In the beechwood areas, whatever the ground vegetation, there is a layer of leaf-litter which gives a dark background. I have not found *hortensis* in plateau beechwoods, although *nemoralis* is often present.

(iv) *Other deciduous woods*. This is a heterogeneous class, including all those woods that do not fit into the last category. Boarstall Wood is predominantly oak, Uffington is oak and hawthorn. Derry Hill Great Wood is open beech with ash and conifers. Wychwood, Rockley Copse, Guiting Wood and Elsfield Covert are very mixed, with hawthorn, oak, ash and hazel. Elsfield Covert, in addition, is damp and boggy, with clumps of *Equisetum*. In all cases the snails were collected in areas of dense ground vegetation, generally either willowherb or nettles. The background is usually less dark and less uniform than in the beechwood areas. Elsfield, however, is very dark indeed.

(v) *Fens*. Samples were taken in three calcareous fens. The collecting areas at Marcham and Headington Wick are in long rushes, and the backgrounds are uniform dark brown. Shippon is greener and much more varied, with grass, nettles, and other herbage.

(vi) *Ivy*. The collections included here were taken beneath ivy (*Hedera helix* L.). The background is very dark brown, almost black; the earth being bare and shaded by a close cover of ivy leaves. Beckley is the most uniform habitat. At Cassington and Mickleham the areas of ivy are fringed by grass. At Mickleham and Woodcote there is some penetration of the cover by umbellifers. The Sonning sample was collected from a bank of ivy within a mixed beech and ash wood.

3. RESULTS

The composition of samples is given in tables 1 and 2. Only live and predated adults are included. Young shells are not used in the tables because fusions of bands cannot be scored among them. Unbroken dead adults are excluded because the mode of death is not known, and therefore the direction of possible errors cannot be predicted (see below). Furthermore, in one colony—Dragons Hill—the dead unbroken shells showed a significantly higher proportion of banded forms than did the live adults ($p < 0{\cdot}005$).

Among my samples, no significant differences were observed between live and predated adults. This does not, of course, argue against the hypothesis of visual selection by predators. A force of

TABLE 1—*The composition of*

(a)	(b)				(c)		(d)		(e)		(f)	(g)	(h)
Locality	Yellows				Pinks		Browns		A		var. *lurida*	Shells with fusions	Total
	12345	00300	00000	Others	12345	00000	12345	00000	12345	Others			
Grass													
1. Silbury Hill, A	159	...	70	2	...	...	27	2	...	...	...	143	260
2. Silbury Hill, B	83	...	32	...	...	...	5	2	...	...	...	50	122
3. Silbury Hill, C	46	...	41	...	...	2	2	...	...	...	...	12	91
4. Silbury Hill, D	53	...	23	...	...	...	1	1	...	...	...	5	78
5. Dragons Hill	60	...	259	4	...	...	...	...	...	...	...	25	323
6. Walker's Hill	7	...	22	...	...	...	...	1	...	...	...	1	30
7. Morgan's Hill	14	...	9	4	...	10	...	...	...	...	*	10	37
8. Three Barrows	19	...	55	...	...	...	3	2	...	...	...	7	79
9. The Ball, Pewsey	29	...	32	...	4	...	...	...	...	...	...	10	65
10. Chisledon-Ogbourne	161	...	142	6	...	7	3	2	4	...	...	5	345
11. Wheatley	80	...	48	1	...	...	...	4	...	...	...	18	133
12. Cowley-Chislehampton	21	...	...	...	...	5	...	4	...	...	...	...	30
13. Wooton-Abingdon A	51	...	35	2	...	8	...	...	1	...	...	4	97
14. Woodperry Corner	37	...	28	...	...	...	...	...	6	...	*	5	71
15. Wheatley-Holton	51	...	32	5	...	...	...	...	...	...	...	10	88
16. Kingstone Coombes	41	...	1	2	...	...	...	...	...	...	...	24	44
17. Etchilhampton	18	...	30	...	...	...	...	...	...	...	...	9	48
18. Kingston Bagpuize-Standlake	11	...	11	1	...	1	...	...	...	...	...	3	24
19. Watlington Hill	...	...	6	...	...	...	...	...	...	...	...	...	6
20. Forest Hill-Stanton	8	...	13	...	...	...	...	...	...	...	...	...	21
Total	949	...	889	27	4	33	41	18	11	...	2	340	1972
Hedgerows and Rough Herbage													
1. Cumnor	43	...	7	1	...	...	...	...	1	...	*	6	52
2. Wootton Rivers	17	...	...	...	2	2	...	1	...	...	*	1	22
3. Marston-Elsfield	22	...	...	...	...	...	...	...	4	...	*	6	26
4. Stowood Crossroads	25	2	8	1	...	2	...	2	1	...	...	6	41
5. Oare Hill A	133	...	14	65	...	...	...	...	...	...	*	27	212
6. Oare Hill B	5	...	...	...	...	...	...	...	...	...	...	1	5
7. Derry Hill A	30	...	9	...	...	3	...	...	2	...	...	8	44
8. Rockley, Berks	17	2	9	1	...	4	...	...	...	...	...	3	33
9. Wooton-Abingdon B	136	21	52	5	...	10	...	...	5	1	*	14	230
10. Swerford	46	...	12	1	...	...	...	...	...	...	...	26	59
11. Christmas Common	7	...	38	...	...	...	...	...	2	...	...	...	47
12. Fiddler's Hill	174	...	39	16	...	...	...	...	...	...	*	1	229
13. Springhill	13	...	...	...	...	...	...	...	1	...	*	...	14
14. Ashbury Hill	4	...	...	3	...	...	...	...	12	9	*	1	28
15. Derry Hill B	6	...	7	...	...	12	...	...	...	...	...	2	23
Total	678	25	195	93	2	33	...	3	28	10	8	102	1067

random samples of C. hortensis.

(i)	(k)	(l)	(m)	(n)	(o)	(p)	(q)
Per cent. Yellows (inc. A)	Per cent. Pinks	Per cent. Browns	Per cent. A	Per cent. "Effectively unbanded"	Per cent. Yoooo	Per cent. Fusions in 12345 and others	Further details
							A = var. *arenicola*
88·8	...	11·2	...	27·7	26·9	76·1	2-10345
94·3	...	5·7	...	27·9	26·2	56·8	
95·6	2·2	2·2	...	47·3	45·1	25·0	
97·4	...	2·6	...	30·8	29·5	9·4	
100·0	...	...	...	80·2	80·2	39·1	4-10345
96·7	...	3·3	...	76·7	73·3	14·3	
73·0	27·0	...	...	51·4	24·3	55·6	3-00345, 1-02345
93·7	...	6·3	...	72·2	69·6	31·8	
93·8	6·2	...	...	49·2	49·2	30·3	
96·3	2·2	1·5	1·2	48·0	43·7	2·9	2-10345, 1-12045 2-02345, 1-00345
97·0	...	3·0	...	39·1	36·1	22·2	1-10345
70·0	16·7	13·3	...	30·0	...	...	All pinks have black lips
90·7	9·3	...	1·0	45·4	36·1	7·4	2-10345 All pinks have black lips
100·0	...	...	8·5	47·9	39·4	11·6	
100·0	...	...	...	36·4	36·4	17·9	3-10345, 2-00345
100·0	...	...	...	2·3	2·3	55·8	2-10345
100·0	...	...	...	62·5	62·5	50·0	
95·8	4·2	...	...	50·0	45·8	25·0	1-10345. Pink has brown lip
100·0	...	...	...	100·0	100·0	25·0	Per cent. fusions scored from unpredated dead
100·0	...	...	...	61·9	61·9	...	
100·0	...	...	1·9	14·8	12·9	13·3	1-12045
77·3	18·2	4·5	...	22·7	...	5·3	
100·0	...	...	15·4	15·4	...	23·1	
90·2	4·9	4·9	2·4	36·6	19·6	22·2	1-02300
100·0	...	...	...	17·5	6·6	16·3	15-10345, 3-00345, 1-00340, 11-10045, 16-10005, 16-00005
100·0	...	...	...	...	...	20·0	
93·2	6·8	...	4·5	31·8	20·5	25·0	
87·9	12·1	...	...	45·5	27·3	16·7	All pinks have black lips 1-10345
95·7	4·3	...	2·6	38·7	22·6	9·5	All pinks have black lips 4-10345, 1-12045, 1-A00300
100·0	...	...	...	20·3	20·3	55·3	1-12305
100·0	...	...	4·3	85·1	80·8	...	
100·0	...	...	...	17·0	17·0	0·5	1-02345, 1-10045, 11-10345, 3-00345
100·0	...	...	7·1	7·1	...	...	
100·0	...	...	75·0	75·0	...	3·6	3-10345, 9-A10345
52·0	48·0	...	...	76·0	28·0	33·3	

TABLE 2—*The composition of*

(a)	(b)				(c)		(d)		(e)		(f)	(g)	(h)
Locality	Yellows				Pinks		Browns		A		var. *lurida*	Shells with fusions	Total
	12345	00300	00000	Others	12345	00000	12345	00000	12345	Others			
Beechwoods													
1. Clipper Down Wood	86	...	4	...	...	...	...	...	...	...	*	58	90
2. Hackpen Wood	36	...	5	2	...	...	...	...	...	...	...	8	43
3. Kingstone Coombes	21	...	...	...	...	...	...	...	...	...	...	7	21
4. Danks Down Wood	33	...	8	...	...	...	...	...	...	...	...	16	41
5. Fawley Bottom Wood	8	...	1	...	...	...	...	...	...	...	*	3	9
6. Maidensgrove Wood	9	...	...	1	...	...	...	...	...	...	*	6	10
7. Ward's Hurst Wood	16	...	1	...	...	...	...	...	...	...	...	12	17
8. Aston Rowant Wood	4	...	3	...	...	...	...	7	...	...	...	2	14
9. Savernake Wood	7	...	...	...	...	...	...	...	...	...	...	3	7
10. Rockley Wood	18	...	...	...	...	...	...	...	...	...	...	9	18
11. Manton Wood	8	...	2	...	...	...	...	1	...	...	...	1	11
12. Knoll Down A	29	...	26	...	...	...	...	...	...	...	...	20	55
13. Knoll Down B	10	...	10	...	...	...	...	...	...	...	...	6	20
14. Knoll Down C	12	...	1	...	...	...	...	...	...	...	...	6	13
Total	297	...	61	3	...	...	...	8	...	...	3	157	369
Other Deciduous Woods													
1. Boarstall Wood	17	4	15	...	...	...	1	34	1	...	...	3	72
2. Rockley Copse	60	17	11	...	...	92	...	...	...	...	...	8	180
3. Guiting Wood	11	...	2	...	...	...	...	...	...	...	...	1	13
4. Wychwood Forest	4	...	1	...	3	...	...	...	...	...	...	3	8
5. Uffington Wood	40	...	3	2	...	...	...	...	1	...	*	15	46
6. Derry Hill Great Wood	13	...	8	...	...	7	...	...	...	...	...	9	28
7. Elsfield Fox Covert	12	5	13	...	...	15	...	...	...	...	...	10	45
Total	157	26	53	2	3	114	1	34	2	...	1	49	392
Fens													
1. Shippon	26	...	40	...	...	13	...	...	...	...	...	1	79
2. Marcham	9	...	17	...	...	8	9	11	...	...	...	10	54
3. Headington Wick	33	...	28	...	...	...	...	1	...	...	...	19	62
Total	68	...	85	...	...	21	9	12	...	...	...	30	195
Ivy													
1. Mickleham, Surrey	55	...	26	...	10	6	...	1	...	...	*	37	98
2. Cassington	19	...	3	...	...	...	...	...	...	...	...	13	22
3. Beckley	31	...	...	...	...	...	...	11	...	...	...	25	42
4. Woodcote	18	...	1	...	...	...	...	...	...	...	*	12	19
5. Sonning-on-Thames	11	...	8	...	4	5	5	11	...	...	...	18	44
Total	134	...	38	...	14	11	5	23	...	...	2	105	225

random samples of C. hortensis (*continued*).

(i)	(k)	(l)	(m)	(n)	(o)	(p)	(q)
Per cent. Yellows (inc. A)	Per cent. Pinks	Per cent. Browns	Per cent. A	Per cent. "Effectively unbanded"	Per cent. Yoooo	Per cent. Fusions in 12345 and others	Further details
							A = var. *arenicola*
100·0	...	...	...	4·4	4·4	67·4	
100·0	...	...	...	11·6	11·6	21·1	2-12045
100·0	...	...	...	...	...	33·3	
100·0	...	...	...	19·5	19·5	48·5	
100·0	...	...	...	11·1	11·1	37·5	
100·0	...	...	...	...	...	60·0	1-023(45)
100·0	...	...	...	5·9	5·9	75·0	
50·0	...	50·0	...	71·4	21·4	50·0	
100·0	...	...	...	...	...	42·9	
100·0	...	...	...	...	...	50·0	
90·9	...	9·1	...	27·3	18·2	12·5	
100·0	...	...	...	47·3	47·3	77·0	
100·0	...	...	...	50·0	50·0	60·0	
100·0	...	...	...	7·7	7·7	50·0	
51·4	...	48·6	1·4	75·0	20·8	15·8	
48·9	51·1	...	...	66·7	6·1	13·3	All pinks have black lips
100·0	...	...	...	15·4	15·4	9·1	
62·5	37·5	...	...	12·5	12·5	42·9	
100·0	...	...	2·2	8·7	6·5	34·9	2-10345
75·0	25·0	...	...	53·6	28·6	69·2	
66·7	33·3	...	...	73·3	28·9	83·3	
83·5	16·5	...	...	67·1	50·6	3·8	All pinks have black lips
48·1	14·8	37·0	...	66·7	31·5	55·6	All pinks have black lips
98·4	...	1·6	...	46·8	45·2	57·6	
82·7	16·3	1·0	...	33·7	26·5	56·9	
100·0	...	...	...	13·6	13·6	68·4	
77·5	...	22·5	...	22·5	...	80·6	
100·0	...	...	...	15·9	5·3	66·7	
43·2	20·4	36·4	...	54·5	18·2	90·0	

selection sufficient to account for the observed differences in the distribution of phenotypes *between* populations would not show itself *within* them unless the samples of both live and predated adults were very large indeed.

If the data given in tables 1 and 2 are compared with Cain and Sheppard's (1954) results for *Cepaea nemoralis* from the same region, it is seen that the two species differ profoundly in the distribution of their

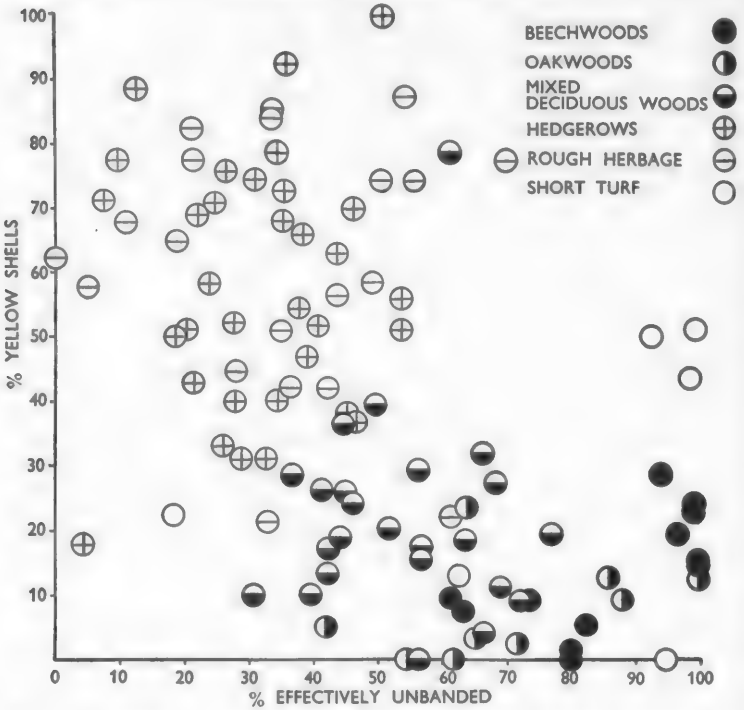

FIG. 2.—*C. nemoralis*. A scatter-diagram showing the relation between percentage of yellow shells, percentage of "effectively unbanded" shells, and the nature of the habitat (after Cain and Sheppard, 1954).

phenotypes. In *hortensis* there is far less variation in the proportion of yellow shells. In nearly every case they form the greater part of the population (columns (*b*) and (*i*)). Albino shells (var. *arenicola*) are more common than in *nemoralis* (columns (*e*) and (*m*)), as are pale-banded forms (column (*f*)) and banded browns (column (*d*)). Banded pinks, on the other hand, are much rarer.

The tables show also that the distribution of phenotypes is not random with respect to habitat. Grasslands, for instance, tend to have a higher proportion of unbanded shells than beechwoods (see column

(*n*)). The converse is true in *C. nemoralis*. Figs. 2 and 3 show this clearly.

Fig. 2 is the scatter-diagram given by Cain and Sheppard (1954). Each spot represents one colony of *nemoralis*. The position of a spot along the vertical axis is determined by the percentage of yellow

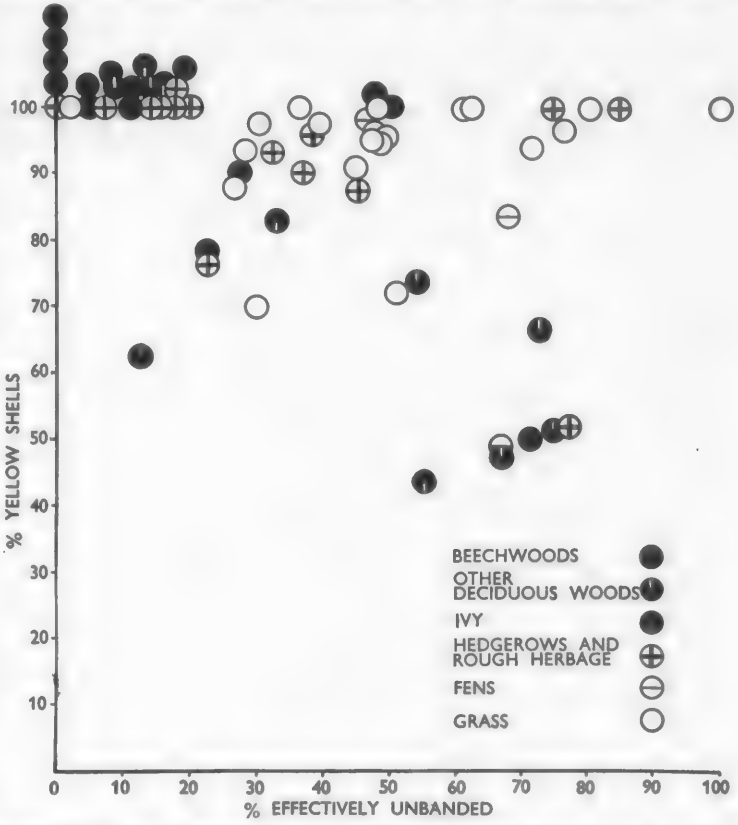

FIG. 3.—*C. hortensis*. A scatter-diagram similar to fig. 2, showing the different distribution of phenotypes in this species.

shells in the colony. Along the horizontal axis its position is determined by the percentage of " effectively unbanded " shells (*i.e.* those shells that have the top two bands missing, including 00300, 00345, 00045, 00000, etc.). On the diagram, colonies from each habitat class tend to be grouped together. The beechwoods lie at the lower right-hand corner, having a low proportion of yellow and a high proportion of unbanded shells. The more open habitats, such as hedgerows and rough herbage, tend towards the left-hand corner. It

must be noted that Cain and Sheppard (1954) class hedgerows and rough herbage as separate groups, but include grasslands in the latter category.

Fig. 3 is a similar diagram, drawn for my collections of *C. hortensis*. Although there is some separation between habitat classes, the grouping

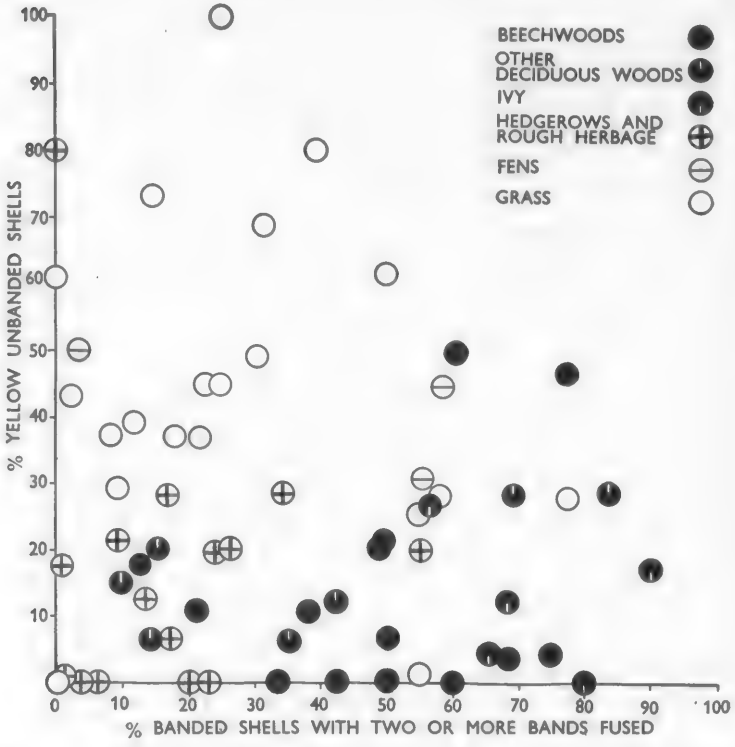

FIG. 4.—*C. hortensis*. A scatter-diagram showing the relation between percentage of yellow unbanded shells, percentage of banded shells with fused bands (see text) and the nature of the habitat.

here is much less distinct. Furthermore, the beechwoods tend to fall on the left-hand side, and the grasslands on the right.

Tables 1 and 2 show that the greater part of the variation of *C. hortensis* is within the yellow colour class. Fig. 4, another scatter-diagram, makes allowance for this. Along the vertical axis are plotted the percentages of yellow unbanded shells (tables 1 and 2, column (*o*)). The horizontal axis gives the proportions of banded shells that have two or more bands fused together (tables 1 and 2, column (*p*)). These proportions are expressed as percentages of the numbers of shells that *could* have two or more bands fused (*i.e.* shells with bands next to

each other—including such forms at 12345, 10045, 12045, 00345, etc., but excluding 00000, 00300, 10005, 10305, etc.).

Fig. 4 shows a clear separation into colour classes. The woodlands, which have few yellow unbanded shells and a high proportion of fusions, are almost completely distinct from the grasslands. The hedgerows and rough herbage, as might be expected, take up a more or less intermediate position. The samples taken under ivy, the darkest habitat, have high percentages of fusions.

The three figures show clearly that *hortensis* populations respond to the influence of the habitat, but that the response is very different from that of *nemoralis*.

4. RELIABILITY OF RESULTS

The results obtained might be affected by several possible errors:

(i) There are, no doubt, random errors of sampling. They would not, of course, give the systematic differences that have been observed between habitat classes. The significance of these differences can easily be demonstrated by non-parametric methods. The samples are arranged in order according to the percentage of shells displaying a particular character, and the distribution of habitat classes about the median percentage is tested by χ^2, the null hypothesis being that, in each habitat, there should be equal numbers of samples falling on either side of the median. For the two characters used in fig. 4 it is found that beechwoods, other deciduous woods, and ivy do not differ significantly from one another and that therefore they can be grouped together for comparison with the other two major classes (hedgerows, rough herbage and grasslands). The distributions of both the percentage of yellow unbanded and the percentage of fusions give 3×2 tables with probabilities that are less than one in a thousand. More refined statistical treatments give even lower values.

(ii) I may have collected too high a proportion of shells that appear conspicuous to the eye. There is no doubt, however, that yellow unbanded shells are more obvious against the dark background of woodlands than are pink, brown, or banded forms—and that shells with their bands fused together are more difficult to see in such situations than are banded shells without fusions. Furthermore, in uniform green grass or herbage the yellow unbanded forms are less obvious than the banded ones, particularly less so than shells with fused bands. Thus any errors of selection by the collector could only tend to obscure the observed differences between habitat classes. This applies also to samples of broken shells collected by thrushes.

(iii) Schnetter and Sedlmair (1953) and Sedlmair (1956) claim to have detected differences in behaviour under experimental conditions between various phenotypes of *Cepaea*. Banded forms of *hortensis*, for instance, were significantly more active than unbanded when the humidity was high. In dry conditions the activity of the unbanded

TABLE 3

Comparison of samples taken from the same places at different times (see text).

Locality	Y	P	▪	12345	F	Total	Date	Comments
Uffington Wood	46	0	0	43	15	46	12.6.57	L.
	21	▪	0	20	6	21	5.6.58	L.
Boarstall Wood	22	0	19	▪	0	41	8.6.57	L.
	15	0	16	11	3	31	1951	T., Cain & Sheppard
Clipper Down Wood	63	▪	0	61	42	63	10.6.57	L.
	27	0	0	25	16	27	10.6.57	T.
Kingstone Coombes Wood	19	0	▪	18	5	19	1951	T., Cain & Sheppard
	21	0	0	20	7	21	29.5.57	T.
Rockley Copse	19	26	0	13	2	45	1952	T., Cain & Sheppard
	63	61	0	43	5	124	14.6.57	T.
Shippon Fen	45	9	0	17	1	54	22.3.57	L.
	531	84	0	259	16	615	21.3.59	T.
Wooton-Abingdon Road	113	6	0	73	5	119	30.4.57	L.
	107	4	0	73	7	111	4.5.57	L.
Oare Hill	191	▪	0	178	26	191	1950	L., Cain & Sheppard
	21	0	▪	20	1	21	6.6.57	L.
Shepherd's Rest	227	▪	0	193	7	227	1957	L., Sheppard
	19	0	0	19	0	19	14.4.58	L.
Wheatley Bridge	63	0	2	39	▪	65	10.4.57	L.
	66	0	2	42	10	68	10.4.57	M.
Dragons Hill	169	▪	0	31	11	169	16.9.56	L.
	54	▪	0	9	5	54	16.4.57	L.
	62	▪	▪	14	8	62	16.4.57	M. & T.
	24	0	▪	6	0	24	12.6.57	L.
	34	▪	▪	6	4	34	16.4.58	L.
	43	0	0	6	4	43	15.4.59	L.
	36	0	0	9	4	36	15.4.59	M. & T.
Silbury Hill, C	87	2	2	48	9	91	6.6.57	L., V.S.
	260	1	10	151	69	271	17.6.58	L., V.C.
	62	1	4	38	16	67	2.9.58	L., Reynolds, V.S.
	224	0	▪	116	37	226	24.10.58	L., Paterson & Murray
	143	▪	5	77	31	148	20.4.59	L., V.S.
Silbury Hill, 8	72	0	10	59	43	82	17.7.57	L.
	17	0	0	12	9	17	14.9.58	L.
White Horse Hill, 1	33	0	0	31	9	33	16.4.58	L.
	52	0	0	52	12	52	15.4.59	L.
Little Hinton	33	0	0	25	4	33	19.4.59	T. (new shells)
	28	0	0	24	4	28	19.4.59	T. (old shells)
Fyfield Roadbank, 1	113	0	0	52	11	113	6.58	L., Armstrong
	84	0	0	39	7	84	6.58	L., Armstrong
	44	0	▪	27	5	44	6.58	L., Armstrong
	58	0	0	34	8	58	6.58	L., Armstrong
	32	0	0	18	4	32	20.4.59	L. On ground
	57	0	0	27	▪	57	20.4.59	L. Climbing
	80	0	1	31	14	81	20.4.59	L.
Fyfield Roadbank, 2	41	0	0	20	2	41	6.58	L., Armstrong
	39	0	0	17	3	39	6.58	L., Armstrong
	49	0	▪	26	▪	49	6.58	L., Armstrong
	57	0	0	27	6	57	6.58	L., Armstrong
Fyfield Roadbank, 3	70	0	10	44	26	80	1.7.57	L.
	51	0	4	34	19	55	1.7.57	T.
	21	0	3	6	3	24	24.9.57	L.
	58	0	5	34	20	63	24.9.57	T.

L = Live, T = Thrush predated, M = Mammal predated, V.S. = Vegetation standing, V.C. = Vegetation cut (scythed). Thanks are due to Drs A. J. Cain, P. M. Sheppard and H. Paterson, and to Messrs A. Armstrong, J. Murray and K. Reynolds for allowing me to use their collections in this table.

variety seemed to be greater, although in this case the difference was not statistically significant. Such experiments do not necessarily reflect what happens in natural populations, but they do show that environmental influence *could* introduce systematic errors into the samples. I have searched for effects of this sort, comparing collections taken from the same colony at various times, under various weather conditions. Table 3 summarises the results of these comparisons. I have included a number of samples that were collected after tables 1 and 2 had been drawn up. Full details of their composition will be recorded elsewhere.

In two localities (Silbury Hill C, and Fyfield Roadbank 3) there were apparent significant heterogeneities between successive samples, but an overall summation of χ^2 (table 4) shows that this extent of

TABLE 4

Sums of χ^2 comparing samples taken from the same colonies at different times—calculated from data of Table 3.

	Banding	Fusions	Colour
Total χ^2 . . .	29·31	33·30	12·58
Degrees of freedom .	35	35	13
Probability . . .	>0·5	>0·5	>0·25

heterogeneity does not in fact exceed chance expectation. In none of the three classes (banding, fusions and colour) does the overall probability fall below 0·25.

I have also compared, in the field, samples taken from the stems and leaves of tall herbage with collections taken from the ground beneath them. As these comparisons were made on the spot, no figures are available, but in fifteen tests no significant differences were observed. It seems that differential behaviour does not significantly and directly alter the composition of samples, although it might well affect the selective advantages of varieties in a population.

We must conclude that the observed grouping of samples from similar habitats represents a genuine influence of the environment upon the composition of *hortensis* populations. This influence could be the result either of direct action by environment upon the phenotype of individual snails, or of natural selection acting upon genetically determined differences—or of both.

5. GENETICS

Many of the obvious colour and banding varieties of *Cepaea* are known to be genetically determined. *C. hortensis* has been bred by Lang (1904, 1912) and *C. nemoralis* by Lang (1908, 1911, 1912), Lamotte (1951, 1954) and Cain and Sheppard (1957). In *hortensis*, as in *nemoralis*,

absence of banding is dominant to its presence, and pink is dominant to yellow (Lang, 1904). The inheritance of brown colour in *hortensis* is not known although, by analogy with *nemoralis*, brown may be expected to dominate pink and yellow. Lang's results suggest that band-fusions may be inherited. Boettger (1950) states that the different combinations of fused bands form an allelic series, but unfortunately he does not provide the necessary data. Forms with thin, interrupted bands are reported to be dominant to the more common thick-banded varieties (Lang, 1912). Lang gives no information, however, about the inheritance of the unpigmented or partially pigmented conditions—although he has shown the former to be recessive in *nemoralis* (1911). Phenocopies, as far as I know, have not been reported by reliable observers.

6. NATURAL SELECTION

Among populations of organisms, spatial or temporal differences in the proportions of genetically determined varieties can be due either to random or to directed processes (see, for instance, Wright, 1955). While " random drift " could, no doubt, occur within populations of *hortensis*, the systematic differences between habitat classes indicate the action of natural selection.

Sheppard (1951) has demonstrated the selection of colour varieties in two populations of *C. nemoralis*. He showed that the percentage of yellow snails killed by thrushes decreased from the middle of April until the middle of May. He gave evidence that this was the result neither of changes of feeding grounds by the thrushes, nor of variations in the populations from which they were collecting. The most obvious explanation was that the thrushes could see the yellow snails less easily as the background became greener.

Goodhart (1958*b*) reports similar seasonal differences in the proportions of pink and yellow *hortensis* collected by thrushes. His data cannot be considered as *conclusive* evidence of selection, for the following reasons:

(*a*) The population from which the birds were collecting was not sampled.

(*b*) The habitat was heterogeneous, and Goodhart did not exclude the possibility of seasonal changes of feeding ground.

(*c*) He compared the proportions of varieties found around " thrush stones " during five successive summers with those collected during the intervening winters. The proportion of pink shells in the two groups appeared to be significantly different ($p < 0{\cdot}01$). The final summer, however, showed a significantly higher proportion of pinks than the other summers ($p < 0{\cdot}01$), and ought not to have been included with them. When it is excluded, the difference between summers and winters is no longer significant ($p > 0{\cdot}05$).

I have criticised Goodhart's work because the hypothesis of visual selection, if it is to be accepted, must be based upon unequivocal

results. Nevertheless, for the reasons given below, it seems very likely that thrushes do, in fact, tend to select the most obvious varieties of *hortensis*, and to overlook those that resemble the background. Shells of this species are found on thrush stones as commonly as are those of *nemoralis*. Both species have similar colour and banding patterns. Since selective predation has been demonstrated in *nemoralis*, it is reasonable to expect the same in *hortensis*.

Predation by thrushes is not, of course, the only possible form of selection. Many other birds eat snails, and they may act in a similar way. Small mammals also prey upon *Cepaea*, and Cain (1953) has suggested that, since they are colour-blind, selection may depend on tone rather than colour. Boettger (1954) and Sedlmair (1956) have reported differences in survival between various phenotypes of *hortensis* and *nemoralis* under adverse conditions. Komai and Emura (1955) have discovered comparable differences in *Bradybaena similaris*.

Polymorphism in *Cepaea* has been in existence since Neolithic times (Diver, 1929) and probably for much longer. The presence of similar colour and banding varieties, not only in all the species of *Cepaea*, but also in the related genus *Pseudotachea* (Sacchi, 1956) suggests that the polymorphism may be very ancient indeed. On a shorter time-scale, Goodhart (1956, 1958*a*) has shown that colonies may persist virtually unaltered in their phenotypic constitution for periods exceeding fifty years. Monomorphic colonies are rare. These facts suggest that much of the variation in *Cepaea* comes into the category of balanced, rather than transient, polymorphism (as defined by Ford, 1945).

For the maintenance of polymorphism there must be forces acting so that the rarer a gene becomes, the greater is its relative advantage. Such a situation occurs if the heterozygote tends to produce relatively more descendants than either homozygote. Another means of maintaining diversity may be provided by predators. If they come to associate common colour varieties with food, they may overlook the rarer forms, even if these stand out against their background. Evidence of effects of this sort is found in the works of Popham (1941, 1942) and Reighard (1908) on predation by fishes.

7. DISCUSSION OF RESULTS

Fig. 3 shows that the distribution of *colour* varieties in *hortensis* is not obviously related to the background from which the samples were taken. The collections with the lowest proportions of yellow shells, however, come from habitats that appear, subjectively, to be the most acid. The snails from Aston Rowant, Boarstall, Marcham, Elsfield and Derry Hill were all collected in piles of rotting vegetation. At Rockley Copse there is not a great deal of dead plant matter, but the area is flat and sandy, with patches of bracken. The Sonning sample seems to be an exception, having been taken under ivy on a

chalk scarp. With the evidence available, the relation between acidity and the incidence of pinks and browns cannot be accepted as fact. It remains an interesting possibility.

Whatever may be the solution of the problem of the distribution of colour varieties, one thing remains certain. *Cepaea hortensis*, in the majority of colonies, has proportionately far fewer pinks and browns than has *nemoralis*. It is remarkable that, in spite of this, the samples seem to match their background.

On dark brown uniform backgrounds, in woods and under ivy, there are high percentages of banded forms with their bands fused together (see fig. 4). The effect of band-fusions is to make the shell appear dark brown in spite of the yellow ground colour, and to make it far less obvious against a woodland background.

In habitats with mixed vegetation (hedgerows and rough herbage) there is a preponderance of unfused banded forms. The disruptive effect of the bands tends to conceal the shells against the criss-cross of stems.

On grass, a uniform light green background, the yellow unbanded forms are least obvious, and most common.

It cannot be expected that the habitat classes will be as distinct in *hortensis* as they are in *nemoralis*. In the first place, *hortensis* is not at all common in woods, with the result that the woodland samples are very small and presumably subject to large sampling errors. Secondly, where *hortensis* does occur it tends to inhabit places where there is a good deal of ground vegetation and where the background is somewhat mixed. *C. nemoralis*, on the other hand, is commoner in woods and often lives where there is little or no ground cover, and where the background is very uniform.

It is therefore surprising how accurate is the agreement between the phenotype-frequency of *hortensis* and the nature of the background. Many colonies that appear, on the evidence of their position on fig. 4, to be aberrant do in fact come from unusual habitats. The beech-woods Knoll Down A and B have an unusually high proportion of yellow unbanded shells but, as I have already mentioned, they are unusually grassy, and the background in places is almost green. The Morgan's Hill downland colony is small in area, isolated and extremely exposed (on the crest of an 800 ft. hill). It has an unusually high percentage of fusions, but nine-tenths of these involve the lower two bands, which are not obvious when the snail is in its normal position on the ground. When a snail is climbing on vegetation the lower bands may be exposed; but at Morgan's Hill none of the plants were more than six inches tall. The distribution of different types of band-fusions will be discussed in a further paper.

The downland sample from Kingstone Coombes, which falls on fig. 4 among the beechwoods, was collected in a small patch of thistles about a hundred yards from a beechwood. Only *nemoralis* occurred in the surrounding grass.

The Cowley-Chislehampton colony, which has no yellow unbanded shells, remains a puzzle. It is small in area, surrounded by colonies of *nemoralis*, and one of its phenotypes, pink unbanded with black lip, is not characteristic of the region (see below). It is conceivable that this colony resulted from the introduction of a very few individuals from elsewhere. The question must, however, be left open.

The Christmas Common hedgerow has a very high proportion of yellow unbanded shells, but it is surrounded by downland, which comes within fifty yards of it. Nearby woods seem to contain only *nemoralis*. It is therefore possible that the unusually high percentage of yellow unbanded shells may be due to gene-flow from the downland.

The explanation of aberrant colonies in terms of gene flow must not be accepted uncritically. It can only be used if the colonies are small in area and numbers, and if the only possible gene flow is from larger colonies of the type to which the smaller ones tend. These conditions are fulfilled in the colonies from Kingstone Coombes and Christmas Common, but there are certainly factors other than background that affect the distribution of phenotypes. Exposure, or something related to it, seems to be one (Clarke, in preparation).

In spite of the two or three colonies that seem not to match their background, the agreement among the other sixty-two or three is very good indeed (see fig. 4).

There are a number of other phenomena, for which complete explanations have not yet been found:

(*a*) Both albinos (var. *arenicola*) and pale-banded forms (var. *lurida*) appear to be more common among hedgerows and rough herbage than they are elsewhere (see tables 1 and 2, columns (*e*) and (*f*)). If only the four major habitat classes are considered, these differences are significant at the 5 per cent. level.

(*b*) In the Oxford region, there are geographical differences in the distribution of certain phenotypes. There is an area of *hortensis* colonies near Abingdon, Berkshire—comprising about twenty square miles and bounded by the villages of Cumnor, Eaton, Fyfield, Marcham, Sunningwell and the town of Abingdon—in which pink shells with black lips occur, but in which yellow shells with black lips have not been found. Black-lipped pinks seem to be absent elsewhere in the Oxford region (excepting, that is, the colony on the road between Cowley and Chislehampton).

The 00300 phenotype appears to be restricted to an area between Rockley and Abingdon, and to another between Oxford and Brill.

Neither black-lipped pinks nor 00300 have been found on the chalk Downs, or on the Chilterns or Cotswolds.

8. DIFFERENCES BETWEEN THE TWO SPECIES

C. nemoralis and *C. hortensis* are very closely related, but nevertheless distinct, species. They can usually be distinguished by shell size,

lip shape, body pigmentation and so on, but the only consistent differences are in the genitalia, particularly in the size and shape of the dart (see Taylor, 1914; Aubertin, 1927; Diver, 1940; and Lamotte, 1951). The chromosome numbers of the two species are identical (Perrot and Perrot, 1938). Hybrids have been obtained between them, but the fertility of crosses is very low (Lang, 1908; Kleiner, 1913). Small numbers of naturally occurring hybrids have been reported (Boettger, 1921), and the possibility of some gene flow between the two species cannot be ruled out.

The polymorphisms in *nemoralis* and *hortensis* are probably determined by genes at homologous loci. In all the experiments so far recorded the dominance relations of the genes for colour and banding are the same in both species. Furthermore, the work of Cain and Sheppard (1954, 1957) suggests that samples from natural populations can be a guide to linkage relations, at any rate in *nemoralis*. If this is true of *hortensis*, we may expect the genes for colour and banding to be linked in this species also, because in my samples the two characters are very significantly associated ($p < 0{\cdot}001$). There is usually a deficiency of banded forms among the pinks and browns.

9. CONCLUSIONS

I have shown that the proportions of different phenotypes in populations of *C. hortensis* can be related to the habitat in which they live, and that this relation is necessarily the result of natural selection, probably of visual selection by predators. The same is true of *C. nemoralis* but, as we have seen, the response of populations to the environment differs in the two species.

If the genes controlling the polymorphisms of *nemoralis* and *hortensis* are homologous, as they appear to be, then the differences of response are, at first sight, puzzling. They can, however, be satisfactorily explained.

I have already pointed out that the two species have slightly different ecological preferences. It might be argued that the selective forces acting upon them are not strictly comparable, and that parallel variation is not to be expected. This can only partly be true. Mixed colonies are fairly common, and in these circumstances the distribution of phenotypes is not the same in each species. In fact, each responds to the environment in its own way (Clarke, in preparation). There might, of course, be differences in behaviour or micro-ecology within a single mixed colony. These could certainly affect the selective values of particular genes, but in visibly uniform habitats they are unlikely to alter the *visual* selective values. *Cepaea hortensis* occurs in a number of uniform beechwoods, in any part of which the brown unbanded variety would be visually superior to the yellow form with fused bands. The latter form is not completely brown; it shows a trace of yellow at the suture. Nevertheless it predominates. This suggests that the difference in response between the two species is due not merely to behavioural

or micro-ecological preferences that cause the two species to occur on visibly different backgrounds.

It has often been pointed out that the action of particular genes cannot be considered apart from their genotypic environment (see, for instance, Mayr, 1954, 1955) and it seems very likely that, for reasons which have nothing to do with the appearance of the shells, the genes for brown and pink are, on the average, less advantageous against the genotypic background of *hortensis* than they are against that of *nemoralis*. In other words, non-visual environmental factors could affect the selective values of the genes in ways that depended upon the genotypic background, producing a low proportion of pinks and browns in most populations of *hortensis*, and a higher one in most populations of *nemoralis*. Such effects could alter the results of visual selection. In beechwoods, for instance, predation by thrushes would act upon *nemoralis* to increase the proportion of brown or pink unbanded shells. *C. hortensis* does not produce a high percentage of browns or pinks, probably for the reasons mentioned above, and therefore the same selective agent would increase the proportion of yellow shells with fused bands. The visible effect, an overall brown appearance, is very similar in both species, but the means of obtaining it are different. The range of variation is more circumscribed in *Cepaea hortensis* than it is in *Cepaea nemoralis*, but both species undoubtedly respond to the colour and uniformity of the background.

This study is regarded as an example of the importance of the genetic environment in determining the selective values of particular genes. It accounts for Lamotte's (1951) inability to find a correlation between the phenotypc frequencies of the two snails, and contradicts his thesis that selection is unimportant in determining the distribution of colour and banding varieties.

10. SUMMARY

1. Random samples were taken from a number of colonies of the polymorphic snail *Cepaea hortensis* Müll. Shells were scored for age, condition, colour and banding.

2. Analysis shows that the proportions of certain varieties can be related to the type of habitat from which the samples were taken. Colonies in woodlands tend to have a high proportion of banded shells with the bands fused together—a condition that gives an overall brown appearance which matches the background of brown leaf-litter. Colonies from grasslands, on the other hand, show a relatively high percentage of unbanded forms, which more closely resemble the uniform green background of grass. The differences between habitat classes are statistically very significant.

3. Works on the genetics of *Cepaea* are reviewed. Many of the colour and banding varieties are known to be genetically determined.

4. There is good evidence that the statistical differences between habitat classes are due to the action of natural selection, particularly

of visual selection by predators, and that the variation comes into the category of balanced, rather than transient, polymorphism.

5. A comparison is drawn between the polymorphism of *C. hortensis* and that of the closely related species *C. nemoralis*, which has been studied by Cain and Sheppard. It is likely that the genes controlling the polymorphisms in the two species are homologous. The comparison shows that although populations of both snails respond to the influence of the habitat, they do so in very different ways. This difference of response is regarded as an example of the importance of the genetic environment in determining the selective values of particular genes.

6. The study provides an explanation of Lamotte's inability to find a correlation between the phenotype-frequencies of the two snails in mixed colonies, and contradicts his thesis that selection is unimportant in determining the distribution of colour and banding varieties.

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NOTES AND COMMENTS

INTERACTION OF MODIFIERS: THE EFFECT OF *PALLID* AND *FIDGET* ON *POLYDACTYLY* IN THE MOUSE

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The polydactylous stock used in this investigation was first described by Holt (1945). Her demonstration that its inheritance is due to a recessive gene, then poorly manifested and incompletely penetrant, was later confirmed by Fisher (1950, 1953). In fact, after selecting for improved manifestation and penetrance, Fisher was able to " classify " polydactyly well enough to show linkage with the locus leaden (*ln*) and demonstrate the existence of linkage group XIII. Further selection has now produced a modifying genetic background which can occasionally produce polydactyly in mice that are not homozygous for the polydactyl gene.

Holt's results and the occurrence of polydactyly in Grüneberg's (1943) fidget stock strongly suggested that the manifestation of polydactyly was influenced by the genes pallid and fidget. This led Fisher to set up a systematic experiment designed to investigate the interactions. The results obtained are the subject of the present note.

The eight possible homozygotes that can be formed with two alleles at each of the three loci, pallid (*pa*), fidget (*fi*) and polydactyly (*py*), were crossed in all the 36 possible combinations, including the homozygous matings by which the stocks were maintained. Each cross produces one of the 27 genotypes that can be formed with two alleles at the three loci and results obtained for the same genotype from different crosses provide a check on whether the parental origin of *py* in relation to *pa* and *fi* has any effect on the incidence of polydactyly. This design also eliminates disturbances that are caused by the poor viabilities of pallid and fidget, as these factors do not segregate in any of the crosses. In its more extreme manifestations polydactyly now occurs to an appreciable extent on the fore as well as the hind feet. This matter will be the subject of a further communication. The data discussed below involve hind feet only.

The reciprocal crosses used provided no evidence for any maternal effect in these stocks. There were no sex differences, and the parental origin of *py* in relation to *pa* and *fi* had no effect on the incidence of polydactyly. It should, however, be pointed out that only 14 out of a total of 1240 *pypy* mice were normal and that such a high penetrance may obscure this kind of effect.

The number of mice showing polydactyly only on the left and only on the right hind feet is shown in table 1. There is suggestive evidence that the relative proportion of mice affected on the left feet only decreases as the number of *py* genes increases. Data of Holt (1945), indicate a similar effect with increasing polydactyl manifestation.

Test of linear regression with the number of *py* genes gives

$$\chi_1^2 = 3{\cdot}95 \quad P \simeq 5 \text{ per cent.}$$

This suggests that the left foot is less readily affected on its own than the right foot, so that with increasing polydactyl manifestation there is a decrease in the relative number of mice affected on the left foot only and a corresponding increase in the number affected on both feet.

The effects of the genes *pa* and *fi* on the manifestation of polydactyly are most clearly illustrated by the results from mice that are ++ and +*py* at the *py* locus. These are presented in condensed form in table 2, in which no distinction is made between different forms of polydactyly (unilateral or bilateral, etc.). With respect to pallid and fidget the only distinctions made are between genotypes homozygous at either or both of these loci, genotypes heterozygous at either or both loci and the homozygous normal controls. No further distinctions are useful because the data are inadequate to detect any specific differences there may be between the effect of pallid and of fidget. There is no doubt of the significant association of both pallid and fidget with polydactyly. Previous evidence for the effect of fidget was obtained by Wallace (1954) and by Truslove (1956).

TABLE 1

Relative incidence of polydactyly on left and right hind feet

Genotype at *py* locus	Right only	Left only	Per cent. Left only
++	76	23	23·2
+*py*	156	33	17·5
pypy	62	8	11·4
	294	64	

Double heterozygotes having the *pa* and *fi* genes from different parents show no difference in incidence from individuals heterozygous for any one of these genes. If the effect of *pa* and *fi* were due to a modifier linked with both *pa* and *fi*, which lie on the same chromosome, such double heterozygotes should have a polydactyl manifestation similar to that of the mutant homozygotes. It therefore seems unlikely that the effect of *pa* and *fi* is due to linked modifiers unless there is one very close to each of these loci.

There is a greater difference in incidence between the homozygous mutants and the heterozygotes than between the heterozygotes and the homozygous normal controls. This suggests the possibility of an actual physiological interaction between the pallid and fidget phenotypic conditions and the polydactyly, as opposed to a simple dosage effect of the *pa* and *fi* genes.

The polydactyl incidence obtained by Holt and Wright (1946) in a cross of a *pypy* mouse with a fidget from Grüneberg's stock was 69 per cent., whereas in the present experiment the cross *fifi* × *pypy* gave an incidence of only 11 per cent. This contrast provides satisfactory evidence for the presence of the gene *py* in Grüneberg's stock. Truslove's (1956) evidence for the association of fidget and polydactyly in his stock supports this conclusion.

It is clear that the modifying genetic background, including in particular the genes *pa* and *fi*, can produce polydactyly in the absence of the major

polydactyl gene *py*. Such a situation may be expected to occur whenever there has been selection of a modifying genetic background favouring the expression of a particular major gene. The cross fertilisation between self-fertile homostyles in natural populations of *Primula vulgaris* (Bodmer, 1958, 1960) may be an example of this effect occurring under natural conditions. The genes *pa* and *fi* must clearly be thought of as partially dominant when we consider them as modifiers of the incidence of polydactyly.

TABLE 2

The effect of pa *and* fi *on the polydactyl incidence of the genotypes* ++ *and* +py

Condition at *pa* and *fi* loci	Polydactyls		Normals	Per cent. polydactyly
Homozygous at either or both loci $\left(\frac{pafi}{pafi}, \frac{pa+}{pa+}, \frac{+fi}{+fi}, \text{and} \frac{pafi}{pa+}\right)$ . .	+*py*	57	163	
	++	53	142	
		110	305	26·51
	Het. $\chi_1^2 = 0{\cdot}03$			
Heterozygous at either or both loci $\left(\frac{pa+}{++}, \frac{+fi}{++}, \frac{pafi}{++} \text{ and } \frac{pa+}{+fi}\right)$.	+*py*	154	1208	
	++	41	377	
		195	1585	10·96
	Het. $\chi_1^2 = 0{\cdot}59$			
Homozygous normal at both loci $\left(\frac{++}{++}\right)$	+*py*	4	167	
	++	8	230	
		12	397	2·93
	Het. $\chi_1^2 = 0{\cdot}09$			

The close agreement of the results from +*py* and ++ genotypes indicates that the gene *py* is still completely recessive. The only evidence for any heterozygous expression of *py* is in the relative incidence of polydactyly on right and left hind feet. Holt (1945) suggested that modifiers favouring the expression of polydactyly in mice would in general be less common than suppressors of polydactyly and supported this suggestion with data obtained from outcrosses of the original stock. It seems that extensive artificial selection for the expression and penetrance of polydactyly has reversed this situation so that " enhancers " are now more common than suppressors. Nevertheless this selection has still not modified the recessiveness of the gene *py*. This supports Fisher's (1950) conclusion that the gene *py* in mice " appears to have advanced very far in the succession of changes needed to suppress its action even in the homozygote ". Such a situation naturally lends itself to the possibility of rapid change in the status of polydactyly in mice providing valuable material for the study of modifiers and their specific effects on the course of development.

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REVIEWS

GENETICS AND COTTON IMPROVEMENT. By Sir Joseph Hutchinson. Cambridge University Press. Pp. 85. 15s.

Thanks to the wise policy of the Empire Cotton Growing Corporation the cotton plant is a classical example in plant genetics and plant physiology. It is also a plant which has been greatly improved by breeding. Over the last half century, the cultivated cotton plant has been transformed from a perennial to an annual, has had its seed hair increased from one inch to two inches in length, and has become world-wide in its cultivation. A genus with diploid species and primitive cultivated types in Africa and India and allopolyploid species and modern cultivated types in America is full of interesting problems to genetics and plant breeding. Sir Joseph Hutchinson has surveyed the history, taxonomy, origin, genetics and improvement in cotton. The emphasis of the survey is on the application of genetics to cotton breeding. It does not set out to be an exhaustive review or a source book for cotton breeders, but attempts to draw certain conclusions from the intensive study of the genetics of cotton.

The study of wild populations has revealed that cotton does not conform to Vavilov's theory of decreasing variation away from the centre of origin. The greatest variation in cotton is not in the centres of origin. Hutchinson relates this difference to the type of breeding system. When a species has spread, and at the same time has adopted an inbreeding system, then its greatest diversity is at the centre. When a species spreads and retains its outbreeding system, it retains its variation at the periphery.

The study of gene substitution is discussed from the excellent example of Knight's work on Black Arm Resistance. The transfer of a single gene for resistance from *Gossypium hirsutum* to *G. barbadense* has resulted in good resistant cultivated varieties. But these varieties are not as good as those lacking the foreign gene except under conditions of bad disease epidemics, which under good cultivation do not often exist. The moral is that one gene or at most a small chromosome segment is not without its ancillary effects and makes this promising method of plant improvement less attractive than it appeared on theoretical grounds.

The crucial problem of the breeder is the type of breeding system to adopt ; this is discussed at some length. Is it better to maintain genetic heterogeneity and preserve the possibility of later improvement or to aim at purity and future stagnation ? Our knowledge of the merits of long-term breeding policies is scanty, so that all concerned in plant and animal improvement should profit by the cotton experiments.

D. Lewis.

DARWIN'S PLACE IN HISTORY. By C. D. Darlington. Oxford: Basil Blackwell. 1959. Pp. 101. 9s. 6d.

The Darwin-Wallace centennial (1858), and the centennial of Darwin's " On the origin of species " (1859), have yielded the hoped-for bounteous crop of books and articles on Darwin and on evolutionism. The appraisals of Darwin's work and personality form a spectrum, from eulogies in veritably

hagiographic style at the " red " end, to doubts and critical questioning of the originality of many of Darwin's teachings at the " violet " end. The book under review inclines towards the " violet " extremity. The author's thesis is that " It seems incredible that the apostle of evolution should have been so deficient in historical sense ; so much so that, although deeply interested in his own priority, he never realised that his own ideas were second hand. He thought he had worked them out himself, even when he had only sorted them out. Moreover, his ideas were less clearly sorted out and less clearly maintained than the ideas of those who first thought of them."

With bold strokes of his pen, the author traces the " second hand " ideas of Charles Darwin to Erasmus Darwin, Lamarck, W. Lawrence, E. Blyth, J. C. Prichard, W. Ch. Wells, P. Mathew, Ch. Naudin, and R. Chambers. The fairly long Appendix (pp. 75-94) to the relatively short book contains well-chosen quotations from some of these first-hand sources, the more useful since to most biologists the originals are not readily accessible. The book under review has all the stylistic brilliance, hard-hitting thrusts, and razor-sharp dialectics for which its author is deservedly famous. One may or may not agree with his opinions and evaluations, but there is no denying that the book will be exciting reading to some, nettling to others, but valuable to all who are interested in the history of ideas, and particularly in the intellectual climate under which the tree of modern evolutionism started its most vigorous growth.

History of science should be concerned with much more than priority claims of this or that scientist ; it may even be argued that such claims may as well be relegated to autobiographies and obituaries. What we really want to understand is how the scientific movement as a whole and its many branches and tributaries progress onward despite their meandering courses. And ultimately we must face the mystery of the creative act in the mind of an individual scientist, and of the collective creative process in the scientific community. Ideas grow and change gradually ; where and how an idea was foreshadowed ; how it became recognisable ; when and how it became useful ; and what nurtured its growth—these are matters of real interest. Now, it cannot be gainsaid that in recent years we came to appreciate more clearly than ever before how widespread were the germs of the evolutionary ideas during the time when " On the origin of species " was in gestation. Loren Eiseley has exhumed the writings of Edward Blyth, who had all but the name for a theory of natural selection, but who used it to uphold the doctrine of permanence of species. We owe thanks to Darlington for having directed, or re-directed, our attention to the works of other pre-Darwinian proto-evolutionists. Not all of his interpretations can, however, be accepted without reservations.

Darlington infers that the writings of Erasmus Darwin " prompted " Malthus to write his work on populations, and cites approvingly Samuel Butler's opinion that they converted Lamarck to his belief in transformation of species. The interesting essays of Wells, Lawrence and Prichard are traced also to Erasmus Darwin, although none of the three authors acknowledged their indebtedness to this source. The book of Lawrence was " inspired, we can hardly doubt, by Erasmus Darwin and encouraged by Prichard ". Mathew had " evidently " read Lawrence. Blyth " might have picked up " ideas from Lawrence or Prichard (whom he cites), or from Erasmus Darwin

(whom he does not cite). Spencer surely read Lamarck, and so did Wallace. Darwin presumably read all, but did not see fit to divulge which ideas he got from whom.

All the above inferences may well be correct; but on the other hand they may not be, and proof or disproof will in the nature of things be hard to come by. The writer A may have actually read and copied some ideas from the publication of B; or A may have merely heard about these ideas from a third party, C, who may or may not have mentioned B's authorship; again, these ideas may have become lodged in A's brain long after the reading of B or the conversation with C have been forgotten; and finally, A may have re-invented them independently of direct or indirect influence of B. It is a fact of life that man is conscious of only a part of his thinking processes; it requires effort to trace the sources of one's own political, philosophical, scientific, and other ideas, not to speak of those of anybody else. Finding out whether evolution has occurred, and if so, what brought it about, occupied Darwin understandably more than facilitating the task of the future historians of evolution theories. This does not mean, of course, that ". . . one of the greatest of our figures should not be dissected, at least by one of us". By all means, let us dissect and study Darwin's work and personality; but in so doing, should we not hold him entitled to the benefit of doubt before we conclude that "Darwin was slippery"?

THEODOSIUS DOBZHANSKY.

BLAKESLEE: THE GENUS DATURA. By A. G. Avery, S. Satina, and J. Rietsema. New York: Ronald Press. 1959. Pp. xii+289. $8.75.

When Dr A. F. Blakeslee died in 1954 he had devoted forty years largely to the study of *Datura*. Between 1915 and 1943 working at the Carnegie Institution and directing numerous collaborators, he had published 154 papers; three also had been published by John Belling on the chromosomes of *Datura*. Since 1944, 71 other papers have appeared by various authors. It was, however, the work of Belling between 1920 and 1927 which inspired the whole of the later development. Abnormal "mutant" plants had been discovered by B. T. Avery between 1915 and 1920. Belling found that these were not due to gene mutation but to trisomic and other whole-chromosome variants. In 1921 he classified them and in the same year a haploid *Datura*, and the first haploid flowering plant, was discovered. The other work on the implications of unbalance, structural change and polyploidy followed.

Blakeslee's contribution to the following years was a discriminating judgment, forceful management and unremitting, repetitive, publication. He believed in keeping the work (and publication) entirely in his own hands: he would part with nothing. This policy of a closed shop his successors (headed by Dr H. H. Plough of Amherst College) are to be congratulated on reversing. They offer seeds of the *Datura* stocks to their colleagues throughout the world.

The present book represents an authorised version of the *Datura* work of the kind Dr Blakeslee would have liked. As such it is a period piece; but it is also a record of experimental versatility implemented with prudence and thoroughness. It reveals innumerable interesting details such as the chromosome chimaeras, the feeble hexaploids and octoploids, the new types

of chlorophyll, the pollen-transmitted " quercina " virus, the methods of controlling pollen and embryo growth. And it is admirably illustrated and fully referenced.

We can now look back on the work as a whole. What is most striking about it is the deep freeze into which the chromosome work descended when Belling departed. Analysis stopped. Terminology congealed. Humps or frying pans remained. Chiasmata were never admitted. The number of plants examined increased by hundreds and thousands. For the study of trisomics in progenies alone I estimate that 99,243 plants are represented in table 4. Here are enumerated primary and secondary trisomics. But what are these secondary trisomics? And how do they arise? Not a word is said.

Yet if we examine the data we find them concealing a variety of novel and instructive indications. Following is an extract from table 4 (p. 96):

Trisomic parent	Selfed progeny : trisomics			
	Parental extra chromosome		Other extra chromosome	
	$2n+1$	$2n+iso$	$2n+1$	$2n+iso$
19·20 . . .	151	7	102	4
1·2 . . .	421	6	27	0
Other ten types .	6169	7	145	4
	6941	20	274	8

We see that when the 19·20 chromosome (and to a less extent the 1·2 chromosome) is the extra chromosome of the parent, it produces a higher frequency of trisomics in respect of *other* chromosomes than do the other types. Why? This is what we expect if the 19·20 trisomic has its chromosome pairing upset, *i.e.* has fewer chiasmata and more univalents for all chromosome types. But we know that iso-chromosomes arise in other plants when univalents appear at meiosis. In fact 19·20 and 1·2 yield a proportionately higher frequency of " secondary trisomics " in their progenies also. This removes any doubt there could be that " secondary trisomics " arise by the formation of iso-chromosomes.

Thus this book on *Datura* might well prove a rich quarry of information for those who are inclined to excavate it. But perhaps none of those who are so inclined will know how to translate into modern speech the vivid phrases in which the Jimson Weed was first explained to the world.

C. D. DARLINGTON.

DREISSIG JAHRE ZÜCHTUNGSFORSCHÜNG. By Professor Dr W. Rudorf. Stuttgart: Fischer Verlag. 1959. Pp. 241. DM. 27.

Erwin Baur was the organiser of plant breeding and in some respects the organiser of genetics in Germany. Twenty-five years ago on 2nd December 1933 he met his death prematurely at the age of 58. The aim of this book is to commemorate his work by recording how it happened and what has sprung from it at the present day. Baur established the first great

Kaiser Wilhelm Institut für Züchtungsforschung in Müncheberg, east of Berlin in September 1928. At the end of the war in 1945 a part of the institute under Professor W. Rudorf found a home at Voldagsen near Hanover. In October 1955 this unit, now a Max Planck Institut, was moved to a more spacious site at Vogelsang, close to Cologne, which now serves as headquarters for the organisation whose work is here sketched by the chief investigators.

The first half of the book deals with fundamental studies on genetics, nuclear in *Antirrhinum* and cytoplasmic in *Epilobium*, on chemical and developmental physiology, and on disease-resistance. The second half deals with past, present, and future work on the fourteen main groups of crop plants. Naturally the account is condensed and the second half is concerned with a summary of details. The treatment crop by crop, the references to past problems of administration, and the omission of ideas from outside the organisation, all contribute to prevent any broad or deep view being reached. The reader meets a further difficulty in the illustrations. About 150 photographs give some idea of the scope and achievements of German crop plant breeding. But there is a lack of exact reference to them in the text or in the legends.

Some 400 references to German papers provide a valuable bibliography for plant breeders. C. D. DARLINGTON.

OLD AND NEW BOOKS DEALING WITH GENERAL PLANT BREEDING. By H. de Haan. Reprinted from *Eupythica*, Vol. 7, No. 2, pp. 197-221. July 1958. Wageningen.

This *catalogue raisonné* of general works on plant breeding is classified under twelve languages and will be widely useful. It is illustrated with photographs of notable authors. Clearly it could be enlarged greatly and the compiler's request for additions is most appropriate. C. D. D.

GENETICAL RESEARCH. Vol. 1, Part 1, 172 pp. Feb. 1960. Cambridge University Press. 40s.

We welcome the appearance of a new periodical of Genetical Research. The formation, lay-out and typography follow, with some improvements of detail, those of the *Journal of Genetics* which was published (from 1910 to 1958) by the Cambridge Press. One of the improvements is that it will appear in annual volumes of three parts. The twelve papers of the first number deal with mice (five papers) and rabbits, *Drosophila* and *Paramecium*, *Aspergillus* and *Coprinus*. The longer papers have summaries of varying style. Instructions given to contributors are detailed and well-considered. Too well-considered, perhaps, for experience shows that contributors are impatient readers. Let us hope they will learn better and we shall all profit thereby. C. D. D.

RUSSIAN REVIEW OF BIOLOGY. Vol. 48, No. 1. Pp. 110. Edinburgh and London: Oliver & Boyd. January 1960. 30s. or $5.

Here we have the first part of the English version of the Russian *Review of Biology*, with seven articles. Three concern enzyme chemistry, two immunology, and two are more general statements. One of these is an account

of Cambridge biology; the other, which is supposed to show Lenin's connection with Soviet Biology turns out to be a eulogy of Pavlov on familiar lines. Both of these succeed, for different reasons, in avoiding the mention of genetics. We cannot, therefore, tell readers of *Heredity* what policy is going to be followed in this delicate matter—unless it is a policy of avoidance.

HEREDITY AND EVOLUTION IN HUMAN POPULATIONS. By L. C. Dunn. Cambridge, Mass.: Harvard Univ. Press, and London: Oxford Univ. Press. 1959. Pp. 157+viii. 20s.

This is a most readable book. After first defining the relations between heredity and evolution, Professor Dunn outlines the principles of heredity as they apply in populations as well as within families, and discusses the agencies which determine the genetical constitutions of populations. Then follow accounts of race formation and of the special features of small and isolated communities, the book concluding with a chapter entitled "A Look Ahead".

The book must be accepted within its limitations. In setting out to deal with populations in terms of the individual genes we can detect within them, rather than in terms of the variation to be observed, the author denies himself the great field of continuous variation: supremely important questions such as the level, and prospectively changing level, of intelligence must thus be left undiscussed. But within these limits he succeeds admirably in illustrating the interplay of variation and selection, the significance of inbreeding and isolation, the problems of disentangling the origins of the differences we find, and the complexity of notions such as race. He draws all his material from studies of man and in doing so brings together a great deal of information which will be of value to the geneticist as well as of interest to the general reader, for much of it is recent and some as yet unpublished. Only the broadest of treatments can be given in so small a compass, but the fascinating account of small communities like the Jews of Rome, the Black Caribs of British Honduras and the endogamous groups within Hindu castes will give many of us the wish to read more about them.

In short this is a book to be commended not only to the public for whom it was written, but also to geneticists themselves, for the interest and information it provides. One geneticist has certainly read it with both pleasure and profit.

KENNETH MATHER.

GENETICAL SOCIETY OF GREAT BRITAIN

ABSTRACTS of Papers read at the HUNDRED AND THIRTY-SECOND MEETING of the Society held on 24th and 25th MARCH 1960, at UNIVERSITY COLLEGE OF NORTH STAFFORDSHIRE, KEELE

INTER-RELATIONS BETWEEN GENOTYPE, DEVELOPMENT AND ECOLOGY IN THE GROWTH OF *DROSOPHILA*

F. W. ROBERTSON

Institute of Animal Genetics, Edinburgh

At first sight genetic variation of body size appears amenable only to statistical description and analysis. When treated as an aspect of growth and studied in different controlled conditions, along with other relevant criteria, such as development time, physiological differences in response to selection and genetic behaviour have to be considered together. Some interesting examples have turned up in experiments relating to gene-environment interaction in *Drosophila*. Thus changes either in growth rate or duration of the growth period may contribute to differences in final body size and such physiological differences have to be allowed for when interpreting genetic differences in reaction to particular environmental changes. When small strains, created by selection for either small body size or small cell size, are back-crossed to the unselected population, the position of the F_1 with respect to the parent sizes is quite different in the two cases and also varies characteristically when the composition of the synthetic diet is altered. By selection under appropriate conditions, the ability to regulate body-size on protein-deficient diets has been greatly increased. These and other data suggest that the inter-relations between genotype and ecological conditions can be best studied by combining the techniques and concepts of both quantitative and physiological genetics.

THE GENETICS OF A PATTERN IN *DROSOPHILA SUBOBSCURA*

J. MAYNARD SMITH and K. C. SONDHI

Department of Zoology, University College, London

An attempt has been made to analyse the genetic mechanisms responsible for the pattern of 3 ocelli and 3 pairs of bristles on the top of the head in *D. suboscura*, by selecting for two different patterns, one symmetrical and one asymmetrical, in a population homozygous for the mutant *ocelliless*, which removes one or more of these nine structures.

The results can be explained if it is assumed that the wild-type pattern depends on two genetic systems, the first responsible for a " prepattern ", determining the positions of the ocelli and bristles, and the second for the formation of a common " precursor " of ocelli and bristles. The wild-type allele of *oc* forms part of the second system, so that in ocelliless flies the precursor is abnormal in amount and distribution. Selection can alter the amount of the precursor, and its distribution along an antero-posterior gradient, but cannot modify its distribution along a gradient from left to right.

INDUCTION OF CHROMATID ABERRATIONS IN *VICIA* WITH ALKYLATING AGENTS IN RELATION TO INTERPHASE CHROMOSOME ARRANGEMENT

C. N. OCKEY

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Chromatid aberrations induced by a single treatment of either TEM or HN_2 have been studied at different recovery times. Aberrations appear in treated cells from 16-36 hours ; this indicates an early interphase sensitive period. The proportion of interchanges decreases while that of intrachanges increases as interphase progresses. Changes in the relative proportions of the different types of intrachange indicate that the size of the chromosome loops involved in the aberrations decrease as interphase advances.

During the early part of interphase aberrations are less localised in certain regions than at later periods. Distribution of the aberrations is never at random however. The regions where aberrations are concentrated can be recognised in cold treated cells as dark staining segments and are often adjacent to the pale staining regions generally referred to as heterochromatin.

The anaphase arrangement of chromosomes appears to be retained throughout early interphase. The sensitivity of the cells during this period depends on several factors some of which control contact between and within chromosomes. The most important of these are degree of coiling, change in nuclear volume, and the amount and relative position of heterochromatin in the chromosomes. There appears to be a two stage process in the production of chromatid aberrations with these agents.

SPERMATOGENESIS IN MAN WITH SPECIAL REFERENCE TO ANEUPLOIDY

O. J. MILLER, U. MITTWOCH and L. S. PENROSE

Galton Laboratory, University College, London

Normal human spermatogenesis was studied by Ford in 1957 using histological methods which enabled him to describe accurately the appearance of the chromosomes at meiosis. Using the same techniques the present investigators examined spermatogenesis and meiosis in known instances of aneuploidy. Three were cases of Klinefelter's syndrome, four were cases of mongolism and one was a case of Klinefelter mongolism. Spermatogenesis was shown to be completely inhibited in all the Klinefelter (XXY) cases.

In the four cases of uncomplicated mongolism (trisomic 21) spermatogenesis was present as was previously found by Mittwoch in 1952. Among the new cases varying degrees of spermatogenesic arrest were observed which were correlated with abnormal chromosomal features. These features included aneuploid and polyploid cells containing from 33 to 92 chromosomal bodies. At diaknesis and meiotic metaphase, cells were seen containing 22, 23 and 24 distinguishable ichromosomal bodies, usually 23. Configurations were found which could be easily interpreted as trivalents but univalents and even multivalents appeared to be present in some cells.

MUTAGENIC ACTION OF TRETAMINE IN RATS AND MICE

A. J. BATEMAN

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Tretamine (otherwise known as TEM) is administered i.p. to males which are then mated, and the dominant lethals scored in the pregnancies.

The relative ease with which effects are induced in post-meiotic and pre-meiotic germ cells differs greatly from X-rays. Thus, whilst 500r X-rays produces about

50 per cent. dominant lethals in sperm, it completely sterilises spermatocytes and the later spermatogonial generations (producing sterility of the male for about 2 months), yet a dose of TEM to produce the same mutation rate in sperm has no detectable effect on the fertility of pre-meiotic germ cells.

There is also a species difference in the response of rats and mice to TEM. Rat and mouse spermatids are both hypersensitive to X-rays, yet while rat spermatids are also hypersensitive to TEM, mouse spermatids are highly resistant.

The rat data, in which a wide dose range was used, suggest a threshold effect. It is argued that threshold effects might be characteristic of chemical mutagens.

INCIPIENT SPECIATION IN *LATHYRUS CLYMENUM*

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Lathyrus clymenum grows wild throughout the Mediterranean region, and seed has been received from various botanic gardens in Europe. Cultures of different origins show minor but constant differences in gross morphology, and attempts to make crosses between cultures are much less successful than crosses within cultures. Cultures also differ in their affinity with the closely related species *L. articulatus*. The evidence indicates that *L. clymenum* is in process of dividing into reproductively isolated sections by the establishment of physiological differences which either prevent cross-fertilisation or lead to embryo abortion if cross-fertilisation occurs.

MALE STERILITY IN LABIATAE

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Male sterile forms occur in a proportion of up to 50 per cent. in wild populations of many species of the Labiatae, constituting an outbreeding system.

The presence of the females in the population requires some selective advantage of the female form over the hermaphrodite, but this is less if the inheritance is cytoplasmically controlled than if controlled by a nuclear gene. In all the species examined it has been found that the two sexes are similar in general vigour and the differential floral characters are dependent on the production of a hormone by the anthers of the hermaphrodite. The only difference which seems genetically significant is a greater fertility of the female compared with the hermaphrodite form.

The possible modes of inheritance of the male sterility have not been exhausted in the schemes previously published. The majority of those investigated are determined by nuclear genes, but the mode of inheritance is complex and has not been elucidated. In no case could a single gene be the determinant and it seems that some hypothesis involving selective fertilisation or zygotic lethality is required.

PROGRESS IN THE GENETICS OF DEFECTIVE COLOUR VISION

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Interest by geneticists in colour blindness has recently been revived by its possible uses in the interpretation of sex chromosomal anomalies in man. It is therefore desirable (1) to bring up to date prevalent notions concerning the biochemistry and localisation of colour defect, (2) to revise the current ideas concerning the allelism of the sex linked genes responsible and (3) to mention and to discuss cases of defective colour vision, which do not fit the accepted pattern of inheritance.

THE DEVELOPMENT OF SYNDACTYLISM IN THE MOUSE

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The recessive gene for syndactylism in the mouse (*sm*/*sm*) regularly leads to fusions between digits 3 and 4 on all four feet; digit 2 is also often involved. In addition, some *sm*/*sm* animals have tail kinks. Contrary to what one might expect, the skeleton in this case is only secondarily affected. The earliest manifestation discovered is a hyperplasia of the epidermis of the feet (and sometimes of the tail). This includes the apical ectodermal ridge of the limb buds which is regarded as a stimulatory organ for limb outgrowth by experimental embryologists. Hyperplasia of the ridge is presumably responsible for overgrowth and subsequent deformation of the limb buds which in turn leads to syndactylism. Hyperplasia of the tail epidermis similarly leads to irregularities of tail development. Some general conclusions arising from this situation will be discussed.

LITTER SIZE, OVULATION RATE AND FOETAL MORTALITY IN INBRED MICE

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Litter size in mice characteristically declines on inbreeding. In the absence of selection at any stage, the mean of the original outbred population should be restored when the inbred lines are crossed. The results from one such study will be presented.

When the constituent factors of litter size were examined, ovulation rate had remained unaffected by inbreeding. By implantation, however, significant differences were apparent between inbred and outbred females, but no further differences in foetal mortality emerged.

ASSESSMENT OF THE COMBINING ABILITY OF WINTER WHEAT VARIETIES IN BREEDING FOR YIELD

F. G. H. LUPTON

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Analysis of the yield components of a diallel series of crosses involving six varieties of *Triticum aestivum*, grown in yield trials from F_1 to F_4 is described.

The trials in F_1 and F_2 comprised unselected bulks of each cross, together with the parental varieties. Those in F_3 and F_4 consisted of random selections from each cross, with replicated plots of the parental varieties.

Predictions made from analysis of the results of the F_1 and F_2 trials are compared with estimates of the mean yield and variance in yielding capacity observed in the trials in F_3 and F_4. The value of the analysis of early generation bulk of diallel crosses as a tool in the assessment of the combining ability of varieties of self-pollinating crop is discussed.

NON-COMPLEMENTARITY BETWEEN METHIONINE-SUPPRESSOR MUTANTS WITH 20 PER CENT. RECOMBINATION IN *COPRINUS*

D. LEWIS

Department of Botany, University College, London

A series of recessive mutants, which suppress the requirement of *met-1* cultures for methionine have been tested for recombination and complementarity. The mutants fall into 4-5 loci. All mutants at loci 1 and 2 are non-complementary

between the mutants within each locus, but complementary between mutants from different loci and with mutants from the other 3 loci.

Mutants grouped in the last three loci also agree in general with the rule that non-complementarity only occurs between mutants of the same or very close loci. But some exceptions were found in which the suppressor mutants that are some 20 units apart by recombination do not complement when the + alleles of the two loci are in different haploid nuclei of a dicaryon.

THE USE OF THE ELECTRONIC COMPUTER IN GENETICS TEACHING

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The form of the number in the electronic computer allows precise analogies with genetic systems. Units of the computer may be provided with " chromosomes ", and their " genotypes " given phenotypic expression ; they can reproduce by self- or cross-fertilisation, and their reproduction affected by chance as it would be in nature. Dominance, independent assortment, linkage and crossing-over are easily arranged ; meiosis in structural heterozygotes presents no difficulty. Breeding populations can be simulated in a way which in essential genetic aspects is closely analogous to reality.

Genetic experiments, of essentially the same character as those with living organisms, may be performed with the pseudo-organisms of the computer. Families or populations may be scored by students in the same way that real families would be ; such student participation forms a valuable supplement to more orthodox practical work ; it stimulates imagination and gives an alternative approach to an understanding of genetic systems.

Experiments have included the construction of a chromosome map with eleven genes, by a series of three-point linkage tests (with end, centromere, and chiasma interference); demonstration of the Sewall Wright effect; comparison of evolution (by natural selection) in inbreeding and outbreeding populations; and the evolution of dominance.

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